Chromosome Science **4**: 31-38, 2000

Karyological analysis of the *Eothenomys* sp. from Nagano City, central Honshu, Japan

Masahiro A. Iwasa and Kimiyuki Tsuchiya[1]

Laboratory of Ecology and Genetics, Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan; [1]Experimental Animal Center, Miyazaki Medical College, Kiyotake, Miyazaki 889-1692, Japan

Received February 17, 2000/Accepted July 29, 2000

Abstract. Red-backed voles in low mountain areas in the vicinity of Nagano City, central Honshu, Japan, have hitherto been taxonomically treated as *Eothenomys* sp. since species identification has not been possible due to ambiguity in diagnostic morphological characteristics that can be used to classify voles from Honshu into one of the two *Eothenomys* species, *E. andersoni* or *E. smithii*. We examined the karyotypes of seven individuals of from the Nagano area (altitude: 380-800 m). The karyotype of the *Eothenomys* sp. consisted of 26 pairs of acrocentrics and one pair of metacentrics, and the sex chromosomes, which is also the standard karyotype of *E. andersoni* and *E. smithii*. X chromosomes were comprised of two types, acrocentrics and subtelocentrics, which are known to be frequently observed in *E. andersoni* and *E. smithii*, respectively. G-band patterns of the autosomes and the long arm of the X chromosome of the *Eothenomys* sp. were identical to those of *E. andersoni* and *E. smithii*. In contrast, Y chromosomes in the male specimens (n=3) were small-sized submetacentric and totally heterochromatic, which was the type of *E. andersoni*, and differed from those of *E. smithii*, which were medium-sized subtelocentric and partially heterochromatic. Since the interspecific variation of the Y chromosome was likely to be specific for each of the species, the *Eothenomys* sp. can be regarded as members of *E. andersoni*.

Keywords: Karyotype, *Eothenomys* sp., Nagano, Y chromosome, *E. andersoni*

Introduction

Two species of the red-backed voles, *Eothenomys andersoni* and *E. smithii*, inhabit Japan except for Hokkaido (Kaneko, 1994). *Eothenomys andersoni* is distributed in eastern and central Honshu, while *E. smithii* is distributed in the western part, including Shikoku and Kyushu. In addition, there is an isolated population of *E. andersoni* in the southern part of the Kii Peninsula, Honshu (e.g., Kaneko, 1994). Within each of the two *Eothenomys* species, there seems to be a substantial amount of variation in the morphological characters. Thus, they are sometimes classified into other taxonomic ranks, as suggested by Imaizumi (1979, 1988): Kaneko's (1994) *E. andersoni* is divided into three valid species, "*E. andersoni*" (northeastern Honshu), "*E. niigatae*" (central Honshu) and "*E. imaizumii*" (the Kii Peninsula), and Kaneko's (1994) *E. smithii* into two species, "*E. kageus*" (eastern Honshu) and "*E. smithii*" (western Honshu).

In central Honshu, the two species overlap in their horizontal distributions, but show a parapatric state in their vertical distributions, with narrow sympatric zones (Kaneko *et al.*, 1992; Kimura *et al.*, 1994; 1999). Classification of several local populations in the central Honshu, however, is still being debated because of ambiguity in the morphological diagnostics, such as the relationship between the tail length and hind-foot length, and some skull and dental characters (Kaneko *et al.*, 1992; Kaneko, 1994; Kimura *et al.*, 1994; 1999).

In the 1970's, voles with ambiguous morphological characteristics were collected at quite low mountain areas (420-630 m) in the vicinity of Nagano City, Nagano Prefecture, central Honshu, Japan (Morozumi and Miyao, 1974; Morozumi, 1977; Miyao *et al.*,

Correspondence: Masahiro A. Iwasa.
Tel: +81-11-706-2279.
Fax: +81-11-706-2225.
E-mail: masahiro@ees.hokudai.ac.jp

1979a ; b ; Kaneko, 1981). These voles exhibited overall similarity with Kaneko's (1994) *E. andersoni* in morphological features, although the body size of these voles was remarkably small compared to that of the specimens of Kaneko's (1994) *E. andersoni* which usually occurs in high mountain areas in Nagano Prefecture (alt. > approx. 2,000 m). They were tentatively regarded as either *Clethrionomys andersoni* (= *E. andersoni*) (Miyao *et al.*, 1979a, b ; Kaneko, 1981) or an unidentified species, *Eothenomys* sp. (Morozumi and Miyao, 1974 ; Morozumi, 1977 ; Morozumi and Morozumi, 1988).

In this study, we examined the karyotype of the voles collected from the same localities of Nagano City where the *Eothenomys* sp. was captured before (Morozumi and Miyao, 1974 ; Morozumi, 1977 ; Miyao *et al.*, 1979a). Since *Eothenomys* species are known to exhibit sex chromosome variations that can be used as species-specific markers (Tsuchiya, 1981 ; Obara, 1986 ; Yoshida *et al.*, 1989 ; Kitahara and Harada, 1996 ; Iwasa, 1998 ; Iwasa *et al.*, 1999b), characterization of the sex chromosomes of the *Eothenomys* sp. would provide us useful clues to clarify the phylogenetic and taxonomic relationships of Japanese *Eothenomys* voles.

Materials and methods

Voles and Scientific Names

Seven voles were collected from the three sites which the *Eothenomys* sp. was reported to inhabit (Morozumi and Miyao, 1974 ; Morozumi, 1977 ; Miyao *et al.*, 1979a) and were subjected to karyotyping (Table 1). The specimen numbers and the details of the collecting localities are shown in Table 1 and Fig. 1, respectively.

In this study, we used the scientific names of the Japanese *Eothenomys* species from Imaizumi's classification system (Tsuchiya, 1981 ; Imaizumi, 1988) as follows : the *andersoni*-complex (= Kaneko's (1994) *E. andersoni*) including Imaizumi's (1988) "*andersoni*", "*niigatae*" and "*imaizumii*" ; the *smithii*-complex (= Kaneko's (1994) *E. smithii*) including Imaizumi's (1988) "*kageus*" and "*smithii*", and the *Eothenomys* sp. (from low mountain areas in the vicinity of Nagano City).

Chromosome Analysis

Chromosomal preparations were obtained from bone marrow cells following short-term culture as described by Obara (1982) and Iwasa *et al.* (1999a). Air-dried cells were stained by conventional Giemsa staining, and by C- and G-banding according to Sumner (1972) and Kato and Yosida (1972), respectively, with a slight modification of the latter banding technique. For comparison, individuals of *niigatae* (n=4) and *kageus* (n=4) from central Honshu (Fig. 1) were also examined.

Results

All the individuals of the *Eothenomys* sp. had the diploid chromosome number of 56 (Fig. 2). The karyotypes consisted of 26 pairs of acrocentrics, one pair of metacentrics (the smallest autosomes) and the sex chromosomes. In the sex chromosomes of the *Eothenomys* sp., there were two types of X chromosomes ; large-sized acrocentric X (A-X) and large-sized subtelocentric X

Table 1. Collecting localities and specimen numbers of *Eothenomys* voles examined in this study.

Species*	Collecting locality	Specimen No.	Sex
sp.	Kadosawa, the vicinity of Nagano City (36° 41′ N, 108° 09′ E, alt. 800 m)	KT3143	f
		HEG165-98	f
	Nanamagari, the vicinity of Nagano City (36° 40′ N, 138° 10′ E, alt. 550 m)	KT3144	m
		KT3145	f
		HEG164-98	f
		HEG166-98	m
	Satojima, the vicinity of Nagano City (36° 39′ N, 138° 10′ E, alt. 380 m)	HEG167-98	m
niigatae	Mt. Yatsugatake, Yachiho, Nagano Pref.	HEG220-98	m
		HEG221-98	f
		HEG222-98	f
		HEG223-98	m
kageus	Nanairi, Hinoemata, Fukushima Pref.	HEG193-98	m
	Tomioka, Gunma Pref.	HEG224-98	m
	Shiga-Kougen, Nagano Pref.	HEG225-98	m
	Higashinagura, Shitara, Aichi Pref.	HEG111-98	m

* Scientific species names are according to Tsuchiya (1981) and Imaizumi (1988)

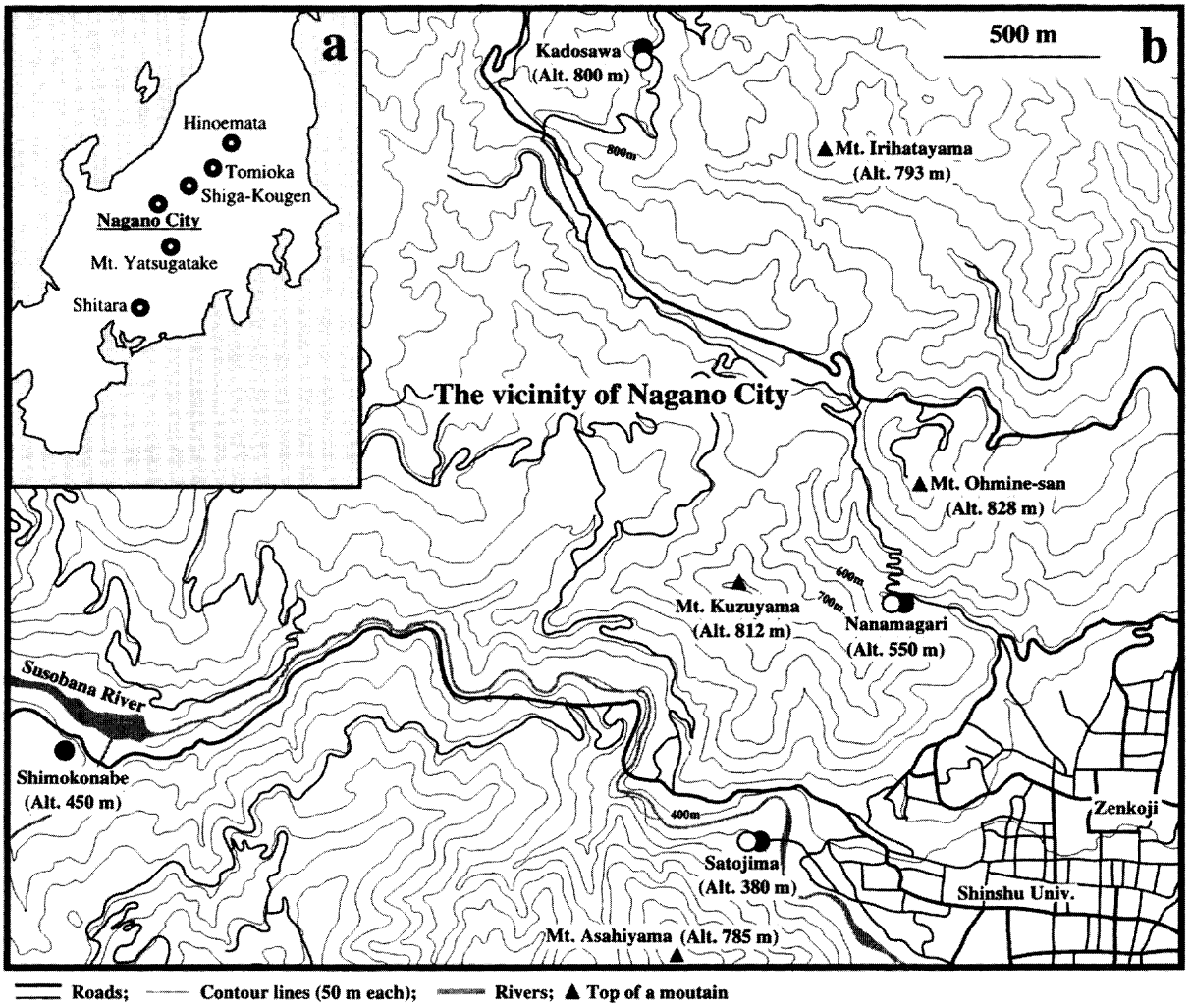

Fig. 1. Collecting localities of the *Eothenomys* voles examined: *niigatae, kageus* and *Eothenomys* sp. (a). The detailed sites of capture of *Eothenomys* sp. in the vicinity of Nagano City (b), solid circles and open circles indicate previously investigated sites (Miyao *et al.* 1979) and our trapping sites, respectively. Locality names are shown in Table 1.

(ST-X), and unique type of Y chromosomes, small-sized submetacentrics (small SM-Y), judging from the statistical analysis of the relative length, arm ratio and centromere index (Tables 2 and 3). All the females (n=4) and males (n=3) carried single sets of A-X/ST-X and ST-X/Y, respectively. From the statistical analysis, the indices of relative lengths of the A-X (5.83±0.48) and ST-X (6.76±0.46) in the *Eothenomys* sp. were quite similar to those of "*niigatae*" and "*kageus*", respectively (Table 2 and Fig. 3). The relative length of the small SM-Y in the *Eothenomys* sp. was 1.46±0.31 which was similar to that of the small SM-Y of "*niigatae*" (1.36±0.19; Table 3 and Fig. 3).

C-bands were consistently located at all centromeric regions in the autosomes and X chromosomes. In contrast, the Y chromosomes had rather variable C-band patterns. The Y chromosomes of the *Eothenomys* sp. and "*niigatae*" were totally C-stained, whereas the Y chromosome of "*kageus*" was C-negative in half of the terminal region of the long arm (Figs. 4a and 5). In this study, it was observed that one male specimen of the *Eothenomys* sp. (specimen No.: HEG166-98) carried a heterozygous C-band in a medium-sized autosomal pair, in which half of the proximal region of the long arm was positively stained by C-banding (Fig. 4b). A heterozygous C- band pattern in an autosomal pair is often observed in red-backed vole species such as *Clethrionomys rufocanus* (Tsuchiya and Yosida, 1974; Kartavtseva *et al.*, 1998).

The G-band patterns of autosomes of the *Eothenomys* sp. were common to those of vole species in the Far East, including *C. rufocanus, C. rex, E. regulus* and Japanese *Eothenomys* voles (the so-called "*rufocanus*" type group) but were different from those of voles from Europe and North America, including *C. glareolus, C. rutilus, C. gapperi* and *C. californicus* (the so-called "*glareolus*" type group) (Fig. 6; Gamperl, 1982; Obara, 1986; Ando *et al.*, 1988; Kashiwabara and

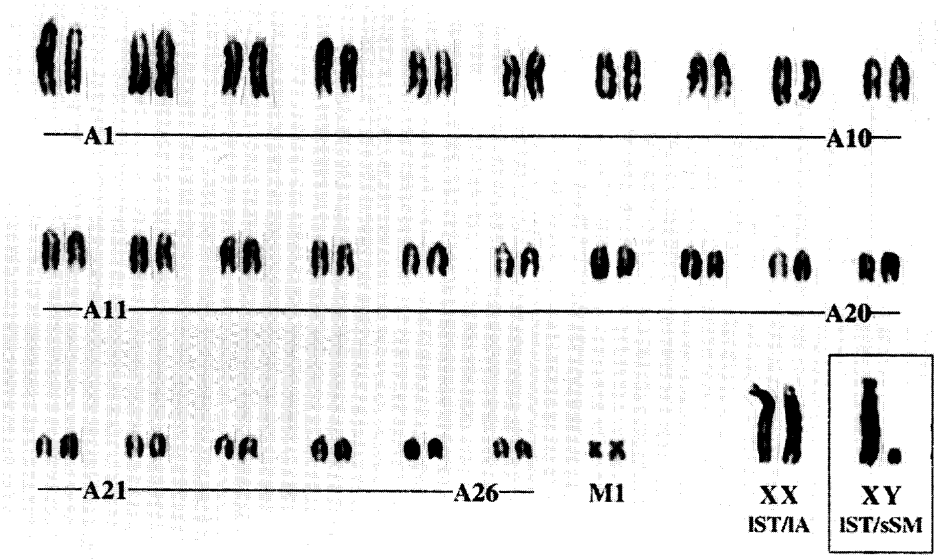

Fig. 2. Conventionally stained karyotype of *Eothenomys* sp. The inset shows the XY chromosomes from a male specimen. lST, large-sized subtelocentric; lA, large-sized acrocentric; sSM, small-sized submetacentric.

Table 2. Morphological features of the X chromosomes in the *Eothenomys* voles examined in this study

Species*	n**	Short arm	Relative length $\frac{X}{TCL}\times 100\pm SD$	Arm ratio $\frac{q}{p}\pm SD$	Centromere position $\frac{p}{p+q}\times 100\pm SD$	Morphology
sp.	30	present	6.76±0.46	7.24±0.53	12.58±0.42	Subtelocentric
	30	absent	5.83±0.48	—	—	Acrocentric
niigatae	25	absent	5.74±0.12	—	—	Acrocentric
kageus	31	present	6.99±0.15	7.19±0.11	12.51±0.05	Subtelocentric

* Scientific names are according to Tsuchiya (1981) and Imaizumi (1988).
** Number of cells observed.

Table 3. Morphological features of the Y chromosomes in the *Eothenomys* voles examined in this study

Species*	n**	Relative length $\frac{Y}{TCL}\times 100\pm SD$	Arm ratio $\frac{q}{p}\pm SD$	Centromere position $\frac{p}{p+q}\times 100\pm SD$	Morphology
sp.	28	1.46±0.31	2.10±0.14	32.31±1.44	Submetacentric
niigatae	25	1.36±0.19	1.91±0.10	34.35±1.23	Submetacentric
kageus	31	3.35±0.34	2.59±0.20	27.89±1.58	Subtelocentric

* Scientific names are according to Tsuchiya (1981) and Imaizumi (1988).
** Number of cells observed.

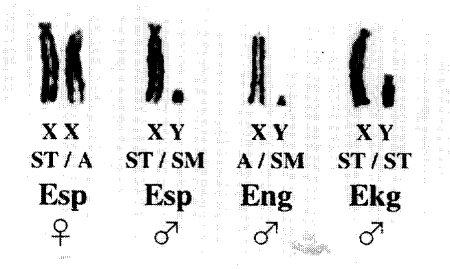

Fig. 3. Conventionally stained X and Y chromosomes of *Eothenomys* sp. (Esp), *niigatae* (Eng) and *kageus* (Ekg). ST, subtelocentric; A, acrocentric; SM, submetacentric.

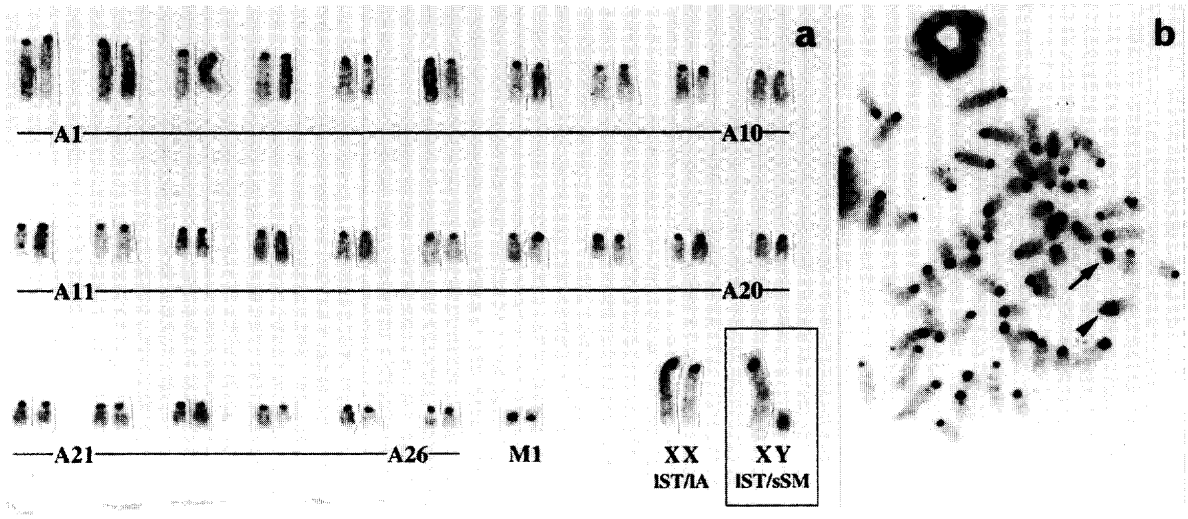

Fig. 4. C-banded karyotype (a) of *Eothenomys* sp. The inset shows the XY chromosomes from a male specimen, and the hetechromatinized autosome observed in specimen HEG166-98. The arrowhead and arrow indicate an autosome with large heterochromatic segments, and Y chromosome, respectively. lST, large-sized subtelocentric ; lA, large-sized acrocentric ; sSM, small-sized submetacentric.

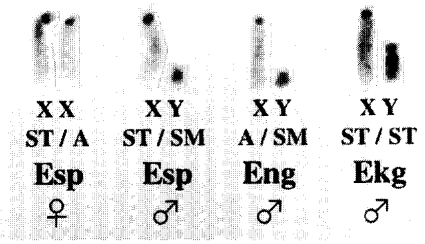

Fig. 5. C-banded X and Y chromosomes of *Eothenomys* sp. (Esp), *niigatae* (Eng) and *kageus* (Ekg). ST, subtelocentric ; A, acrocentric ; SM, submetacentric.

Onoyama, 1988 ; Modi, 1987 ; Modi and Gamperl, 1989 ; Yoshida *et al*., 1989 ; Obara *et al*., 1995 ; Kitahara and Harada, 1996 ; Iwasa, 1998 ; Iwasa *et al*. 1999a). The G-band patterns of the long arm of the X chromosome in the *Eothenomys* sp. were conservative one identical to those of other *Eothenomys* voles, irrespective of the absence or presence of the short arm of the X (Gamperl, 1982 ; Obara, 1986 ; Ando *et al*., 1988 ; Kashiwabara and Onoyama, 1988 ; Modi, 1987 ; Modi and Gamperl, 1989 ; Yoshida *et al*., 1989 ; Obara *et al*., 1995 ; Kitahara and Harada, 1996 ; Iwasa, 1998 ; Iwasa *et al*. 1999a). G-band patterns in the Y chromo-

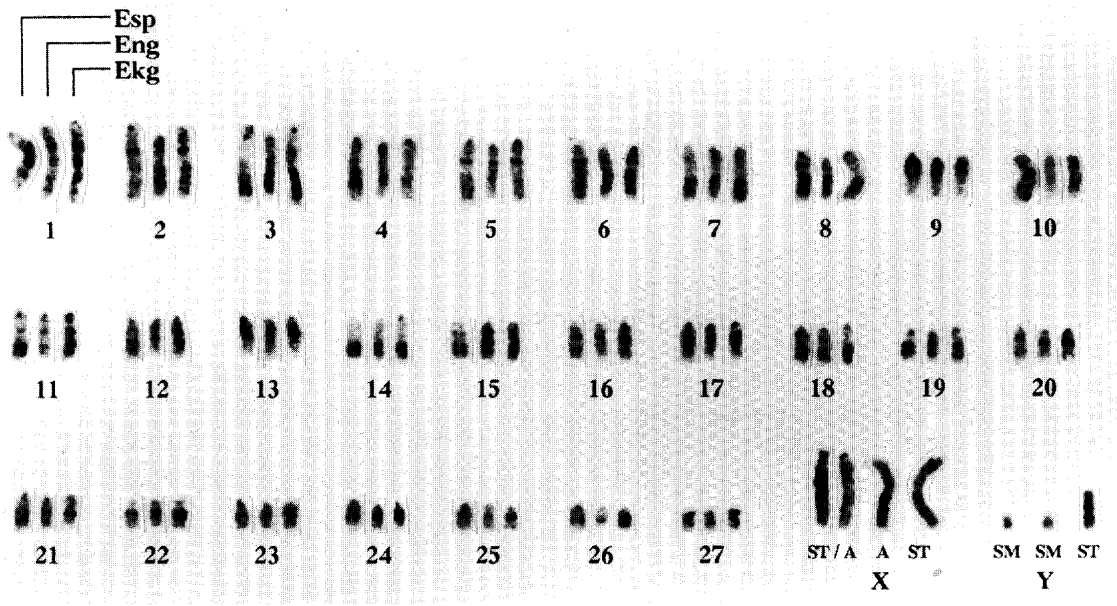

Fig. 6. Pair-matching of G-banded haploid chromosomes among *Eothenomys* sp. (Esp : left), *niigatae* (Eng : middle) and *kageus* (Ekg : right). ST, subtelocentric ; A, acrocentric ; SM, submetacentric.

some were unclear in the *Eothenomys* sp., as in "*niigatae*" (Fig. 6).

Discussion

The Japanese *Eothenomys* voles, including the *Eothenomys* sp., has been shown to carry conserved autosomes but variable sex chromosomes from the present data (Figs. 2 and 3) and the literature (Obara, 1986; Tsuchiya *et al.*, 1986; Ando *et al.*, 1988; Yoshida *et al.*, 1989; Kitahara and Harada, 1996; Iwasa *et al.*, 1999b), as summarized in Table 4. In the Japanese *Eothenomys* voles, hence, there are three types of combinations of sex chromosomes for male individuals; 1) A-X/small-sized Y, 2) ST-X/ small-sized Y and 3) ST-X/medium-sized Y. The former two were common sets of "*andersoni*", "*niigatae*" and "*imaizumii*", while the last one was the typical set of "*kageus*" and "*smithii*" (Table 4; Tsuchiya, 1981; Obara, 1986; Tsuchiya *et al.*, 1986; Ando *et al.*, 1988, 1991; Yoshida *et al.*, 1989; Kitahara and Harada, 1996; Iwasa *et al.*, 1999b). The X chromosomes in the *Eothenomys* voles tend to show a variable state within and among species, and the variation of A-X or ST-X can not be used as a species-specific marker to recognize the *andersoni-* and *smithii*-complexes. Accordingly, the arm ratio and centromere index of the Y chromosomes were also variable in the *andersoni*-complex (Table 3; Tsuchiya, 1981). It has been shown that the morphology of the Y chromosomes varies within and among species of the red-backed voles (Vorontsov *et al.*, 1980; Yoshida *et al.*, 1989; Kitahara and Harada, 1996). However, the overall features of the Y chromosomes, such as relative length (small- or medium-size) and C-band pattern (totally or partially heterochromatic), tend to show good accordance with the current systematics. These two characteristics, therefore, would be useful for species classification (Table 4; Tsuchiya, 1981; Obara, 1986; Ando *et al.*, 1988, 1991; Yoshida *et al.*, 1989; Kitahara and Harada, 1996; Iwasa, 1998). Accordingly, the small-sized and totally heterochromatic Y and the medium-sized and partially heterochromatic Y are considered to be characteristic of the *andersoni*-complex and *smithii*-complex, respectively, irrespective of morphology (arm ratio) of the Y chromosomes (Table 3, Figs. 3 and 5; Tsuchiya, 1981; Obara, 1986; Tsuchiya *et al.*, 1986; Ando *et al.*, 1988, 1991; Yoshida *et al.*, 1989; Kitahara and Harada,

Table 4. Chromosome features of the Japanese *Eothenomys* voles.

Species*	2n	FN	Morphology of X	Size of Y	Morphology of Y	Positive C-band of Y	References
andersoni	56	56	A	Small	M	Total	Tsuchiya (1981) Obara and Yoshida (1985) Obara (1986) Tsuchiya *et al.* (1986) Yoshida *et al.* (1989) Iwasa *et al.* (1999b)
niigatae	56	56	A	Small	SM	Total	Present data Tsuchiya (1981) Tsuchiya *et al.* (1986) Kitahara and Harada (1996)
imaizumii	56	56	ST	Small	M	Total	Tsuchiya (1981) Kitahara and Harada (1996) Iwasa (1998) Iwasa *et al.* (1999b)
kageus	56	56	ST	Medium	ST	Partial	Present data Tsuchiya (1981) Tsuchiya *et al.* (1986) Ando *et al.* (1988) Iwasa *et al.* (1999b)
smithii	56	56	ST	Medium	ST	Partial	Tsuchiya (1981) Ando *et al.* (1988) Ando *et al.* (1991) Iwasa (1998) Iwasa *et al.* (1999a) Iwasa *et al.* (1999b)
sp.	56	56	A/ST	Small	SM	Total	Present data

FN, autosomal fundamental arm number; A, acrocentric; ST, subtelocentric; SM, submetacentrih; M, metacentric.
* Scientific species names are according to Tsuchiya (1981) and Imaizumi (1988).

1996; Iwasa *et al.*, 1999b).

Many studies on the morphology of the *Eothenomys* sp. have also been performed to date but taxonomic classification based on morphology has remained controversial because of conflicting findings by different morphological taxonomists (Imaizumi, 1979; Kaneko, 1981; Miyao, 1981; Miyao *et al.*, 1979a, b; Kaneko *et al.*, 1992; Kitahara, 1995; Kimura *et al.*, 1994, 1999). However, in our opinion, the difference of mammae formula is likely to provide useful information to discriminate the *andersoni*-complex (2+0+2=8) from the *smithii*-complex (1+0+2=6 or 0+0+2=4) (Miyao *et al.*, 1979a, b: Kaneko, 1981). The *Eothenomys* sp., which shows the formula 2+0+2=8 belongs to the *andersoni*-complex type. It is also notable that the *Eothenomys* sp. and the *andersoni*-complex share common characteristics in the enamel patterns of the upper third molar (posterior type: Kaneko, 1981) irrespective of variation in external body sizes (*e.g.*, Morozumi and Miyao, 1974). Moreover, our *Eothenomys* sp. specimens appear to have another characteristic of the *andersoni*-complex in the relationship between hind-foot length and tail length (Iwasa, unpublished data), which has been used to classify both species-complexes by Kaneko *et al.* (1992) and Kimura *et al.* (1994, 1999). We conclude, therefore, that the *Eothenomys* sp. is a member of Kaneko's (1994) *E. andersoni* in taxonomic status judging from the several sets of morphological characteristics (Kaneko, 1981; 1994; Miyao *et al.*, 1979a, b; Kaneko *et al.*, 1992; Kimura *et al.*, 1994, 1999) as well as the Y chromosomal variation.

Acknowledgements

The authors are grateful to Dr. Hitoshi Suzuki (Hokkaido University) for his improving the manuscript and encouragement. We wish to express our gratitude to Drs. Motomi Morozumi, (Board of Education, Chino City, Nagano Prefecture) for his valuable suggestions. We also thank Drs. Yoshitaka Obara (Hirosaki University), Yukibumi Kaneko (Kagawa University), Keisuke Nakata (Hokkaido Forestry Research Institute) and Yoshiyuki Kimura (Fukushima University) for their encouragement throughout this study. Special thanks are due to Dr. Sen-ichi I. Oda (Nagoya University) and Messrs. Shin-ichiro Kawada (Nagoya University) and Akio Shinohara (Hokkaido University) for their co-operation in collecting voles. This report is dedicated to the memory of the late Tetsuro Morozumi who studied the biology of the red-backed voles in Nagano Prefecture.

References

Ando, A., Shiraishi, S., Harada, M. and Uchida, T.A. (1988). A karyological study of two intraspecific taxa in Japanese *Eothenomys* (Mammalia: Rodentia). J. Mamm. Soc. Japan **13**: 93-104.

Ando, A., Shiraishi, S., Harada, M. and Uchida, T.A. (1991). Variation of the X chromosome in the Smith's red-backed vole *Eothenomys smithii*. J. Mamm. Soc. Japan **15**: 83-90.

Gamperl, R. (1982). Chromosomal evolution in the genus *Clethrionomys*. Genetica **57**: 193-197.

Imaizumi, Y. (1960). Colored Illustrations of the Mammals of Japan. Hoikusha, Osaka (*in Japanese*).

Imaizumi, Y. (1988). A World List of Mammals with Japanese Names. Heibonsha, Tokyo (*in Japanese*).

Iwasa, M.A. (1998). Chromosomal and molecular variations in red-backed voles. Honyurui Kagaku [Mammalian Science] **38**: 145-158 (*in Japanese with English abstract*).

Iwasa, M.A., Han, S.H. and Suzuki, H. (1999a). A karyological analysis of the Korean red-backed vole, *Eothenomys regulus* (Rodentia, Muridae), using differential staining methods. Mammal Study **24**: 35-41.

Iwasa, M.A., Tsuchiya, K. and Suzuki, H. (1998). Genetic analyses of the *Eothenomys* sp. from Nagano City, Japan. *In* Annual Meeting of the Mammalogical Society of Japan, Abstract, p. 134 (*in Japanese*).

Iwasa, M.A., Obara, Y., Kitahara, E. and Kimura, Y. (1999b). Synaptonemal complex analyses in the XY chromosomes of six taxa of *Clethrionomys* and *Eothenomys* from Japan. Mammal Study **24**: 103-113.

Kaneko, Y. (1981). External, cranial, and molar characters of red-backed vole collected from lower mountain areas in Nagano. *In* Annual Meeting of the Zoological Society of Japan, Abstract, p. 663 (*in Japanese*).

Kaneko, Y. (1994). Rodentia. *In* A Pictorial Guide to the Mammals of Japan (ed. Abe, H.), pp. 81-110 and 168-182, Tokai Univ. Press, Tokyo (*in Japanese*).

Kaneko, Y., Nakashima, T. and Kimura, Y. (1992). Identification and vertical distribution of two species of *Eothenomys* on Ryo-Hakusan mountains, central Honshyu, Japan. Bull. Gifu Pref. Mus. **11**: 23-34 (*in Japanese with English abstract*).

Kartavtseva, I.V., Pavlenko, M.V., Kostenko, V.A. and Chernyavskii, F.B. (1998). Chromosomal variation and abnormal karyotypes in the red backed mouse *Clethrionomys rufocanus* (Rodentia, Microtinae). Russian J. Genet. **34**: 928-935.

Kashiwabara, S. and Onoyama, K. (1988). Karyotypes and G-banding patterns of the red-backed voles, *Clethrionomys montanus* and *C. rufocanus bedfordiae* (Rodentia, Microtinae). J. Mamm. Soc. Japan **13**: 33-41.

Kato, H. and Yosida, T.H. (1972). Banding patterns of Chinese hamster chromosomes revealed by new techniques. Chromosoma (Berl.) **36**: 272-280.

Kimura, Y., Kaneko, Y. and Iwasa, M.A. (1999). Identification and vertical distribution of two species of *Eothenomys* in the Oze district, northeastern Honshu,

Japan. Honyurui Kagaku [Mammalian Science] **39**: 257-268 (*in Japanese with English abstract*).

Kimura, Y., Kaneko, Y. and Yoshida, T. (1994). Small mammalian fauna in Adatara mountain regions with special reference to genus *Eothenomys*. Fukushima Seibutsu **37**: 13-19 (*in Japanese*).

Kitahara, E. (1995). Taxonomic status of Anderson's red-backed vole on the Kii Peninsula, Japan, based on skull and dental characters. J. Mamm. Soc. Japan **20**: 9-28.

Kitahara, E. and Harada, M. (1996). Karyological identity of Anderson's red backed voles from the Kii Peninsula and central Honshu in Japan. Bull. Forest. Forest Prod. Res. Inst. **370**: 21-30.

Miyao, T., T. Morozumi and Y. Takada. (1979a). A report of small mammal fauna of Nagano city, Honshu. J. Mamm. Soc. Japan **7**: 305-310 (*in Japanese with English abstract*).

Miyao, T., T. Morozumi, M. Morozumi and Y. Takada. (1979b). A report of small mammal fauna on Mt. Iizuna, Nagano Pref. J. Mamm. Soc. Japan **7**: 300-304 (*in Japanese with English abstract*).

Modi, W.S. (1987). Phylogenetic analyses of chromosomal banding patterns among the Nearctic Arvicolidae (Mammalia: Rodentia). Syst. Zool. **36**: 109-136.

Modi, W.S. and Gamperl, R. (1989). Chromosomal banding comparisons among American and European red-backed mice, genus *Clethrionomys*. Z. Säugetierk. **54**: 141-152.

Morozumi, T. (1977a). A continuation of small mammalian fauna from the Mt. Ohmine-san national forests in the vicinity of Nagano City. *In* Nihon Honyurui Zakki vol. 4, pp. 20-24, Shinshu Honyurui Kenkyukai, Nagano (*in Japanese*).

Morozumi, T. (1977b). A continuation of small mammalian fauna from the area of Susobana River in the vicinity of Nagano City. *In* Nihon Honyurui Zakki vol. 4, pp. 22-24, Shinshu Honyurui Kenkyukai, Nagano (*in Japanese*).

Morozumi, T. and Miyao, T. (1974). Small mammals from the Mt. Ohmine san national forests in the vicinity of Nagano City. *In* Nihon Honyurui Zakki vol. 3, pp 71-76, Shinshu Honyurui Kenkyukai, Nagano (*in Japanese*).

Morozumi, T. and Morozumi, M. (1988). Animals in Shinshu. Shinano Kyouiku-kai Shuppan-bu, Nagano, Japan (*in Japanese*).

Obara, Y. (1982). Comparative analysis of karyotypes in the Japanese mustelids, *Mustela nivalis namiyei* and *M. erminea nippon*. J. Mamm. Soc. Japan **9**: 59-69.

Obara, Y. (1986). G-band homology between the Japanese red-backed vole, *Clethrionomys a. andersoni* and the grey red-backed vole, *C. rufocanus*. Chrom. Inf. Serv. **40**: 7-9.

Obara, Y., Kusakabe, H., Miyakoshi, K. and Kawada, S. (1995). Revised karyotypes of the Japanese northern red-backed vole, *Clethrionomys rutilus mikado*. J. Mamm. Soc. Japan **20**: 125-133.

Sharp, P.J. (1986). Synaptic adjustment at a C-band heterozygosity. Cytogenet. Cell Genet. **41**: 56-57.

Sumner, A.T. (1972). A simple technique for demonstrating centromeric heterochromatin. Exp. Cell Res. **75**: 304-306.

Suzuki, H. (1994). Genetic diversity of ribosomal DNA: Phylogenetic analysis of small mammals. Honyurui Kagaku [Mammalian Science] **34**: 67-79.

Suzuki, H., Iwasa, M., Harada, M., Wakana, S., Sakaizumi, M., Han, S. H., Kitahara, E., Kimura, Y., Kartavtseva, I. and Tsuchiya, K. (1999). Molecular phylogeny of red-backed voles in Far East Asia based on variation in ribosomal and mitochondrial DNA. J. Mamm. **80**: 512-521.

Tsuchiya, K. (1981). On the chromosome variations in Japanese cricetid and murid rodents. Honyurui Kagaku [Mammalian Science] **42**: 51-58 (*in Japanese*).

Tsuchiya, K. and Yosida, T.H. (1974). Chromosome survey of small mammals in Japan. Ann. Rep. Nat. Inst. Genet. (Japan) **21**: 54-55.

Tsuchiya, K., Kimura, Y. and Minato, S. (1986). Comparison of cytogenetics in Japanese red-backed voles. *In* Conservation and Rehabitation of Oze, pp. 97-42, Fukushima Prefectural Project Report on the Conservation of Special Plant Species and Their Habitats, Fukushima Prefecture (*in Japanese*).

Yoshida, I., Obara, Y. and Matsuoka, M. (1989). Phylogenetic relationships among seven taxa of the Japanese microtine voles revealed by karyological and biochemical techniques. Zool. Sci. **6**: 409-420.