ZOOLOGICAL SCIENCE 18: 433–442 (2001)

Geographical Variations in Chromosomes of the Greater Japanese Shrew-Mole, *Urotrichus talpoides* (Mammalia: Insectivora)

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ABSTRACT—Karyotypes of the greater Japanese shrew-mole, *Urotrichus talpoides* (Talpidae), collected from 57 localities in Japan were studied by conventional, G- and C-band staining techniques to elucidate geographical chromosomal variations, the mechanism of changes in chromosomes, and the distribution patterns of karyotypic races. Shrew-mole samples examined could be divided geographically into two slightly divergent chromosomal forms designated as the western and eastern races. These two karyotypic races had the same diploid number (34) and fundamental number (64), but they had autosomes with different make-ups. A comparison of conventional karyotypes showed a distinct intraspecific variation in shape of autosomal pair no. 14 which was classified as subtelocentric in the western race and as metacentric in the eastern race. G- and C-banding analyses revealed that karyotypic variation found in no. 14 pair was involved in pericentric inversion and quantitative changes in constitutive heterochromatin. Intraspecific and geographical variation in chromosomes caused by such karyological events is rare and unique among members of the family Talpidae examined so far. Furthermore, our results demonstrated that the clear boundary between the two parapatric karyotypic races was actually located along the Kurobe-Fuji line in the central part of Honshu, but not along the Owari-Tsuruga isthmian line previously postulated by Tsuchiya (1987, 1988). Zoogeographical implications of the boundary of parapatric distribution in *U. talpoides* are also discussed.

INTRODUCTION

The greater Japanese shrew-mole, *Urotrichus talpoides*, belonging to the subfamily Scalopinae of the family Talpidae is a semifossorial shrew-like mole endemic to Japan at the generic level, being the one and only species of the genus *Urotrichus*. It inhabits mountainous areas from lowlands to highlands in Kyushu, Honshu, Shikoku, Tsushima Island, Goto Islands, and Oki Islands, but not in Hokkaido (Imaizumi, 1970; Abe, 1994). The karyological studies in *U. talpoides* have been done using the conventional and/or differential staining techniques (Tsuchiya and Yosida, 1971; Tsuchiya, 1979, 1987, 1988; Hamada and Yosida, 1980; Kawada and Obara, 1999). *U. talpoides* has the diploid number of 34 and the fundamental number of 64, although a minor difference is found in the chromosomal classification of some elements between the researchers. In the course of karyological investigations, Tsuchiya (1987, 1988) found a karyotypic difference in shape of one autosomal pair between specimens from two localities in Shizuoka and Aomori Prefectures and surmised that populations northeast of the Owari-Tsuruga isthmian line may differ genetically from those southwest of the line. His finding from the conventional karyotype analysis indicated chromosomal variation or polymorphism in this species, which was characterized by two different karyotypes. However, information from only a few localities is insufficient to illustrate comprehensive geographical patterns of karyotypic variation in *U. talpoides*. The actual range of distribution of the chromosomal variants and the mechanism causing such variation still remains to be solved. Knowledges regarding the geographical pattern and mode of karyotypic variation are of importance for better understanding of various evolutionary and zoogeographical aspects of the taxon.

We carried out a chromosomal survey of *U. talpoides* using much more specimens from many various localities in Japan, especially in central Honshu. The purpose of this study is to describe the conventional, G- and C-banded karyotypes of *U. talpoides* in detail, to examine the geographical variation of the chromosomes and to consider a mechanism caus-

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ing such variation. We also paid a special attention to establish a reliable geographical line that separates this species into karyotypically distinct populations.

MATERIALS AND METHODS

A total of 245 individuals of *U. talpoides* were collected from 57 different localities throughout Japan between 1983 and 2000 (Table 1 and Fig. 1) for karyotype analysis. The specimens were identified on the basis of the description of Imaizumi (1970) and deposited in the Laboratory Animal Center, Osaka City University Medical School.

Chromosomal preparations were made from primary lung or tail tissue cultures by standard air-drying methods (Harada and Yosida, 1978). The chromosomes, as defined by Levan *et al.* (1964), were classified into metacentrics (M), submetacentrics (SM), subtelocentrics (ST) and acrocentrics (A), and were arranged by size. The diploid number (2n) was determined on the basis of at least 30 well-dispersed metaphase cells. The fundamental number (FN) was defined as the total number of arms of autosomes. The G-band technique employed was identical with the trypsin digestive method of Seabright (1971), and C-bands were produced by a slight modification of Sumner's (1972) technique.

RESULTS

Conventional staining

The karyotypes were obtained for all 245 specimens from 57 localities examined. All the specimens had 2n=34 format with FN=64. However, two different types of chromosome were recognized in shape of one autosomal pair (no. 14). In the west-type karyotype (Fig. 2A), the autosomes consisted of 12 pairs of medium- to large-sized M elements (nos. 1–12), one pair of medium-sized SM elements (no. 13), one pair of large ST elements (no. 14), and two pairs of small ST elements (nos. 15 and 16). One M pair (no. 5) was characterized by secondary constrictions adjacent to the centromeric region. The X chromosome was a medium-sized SM element, and the Y was a dot-like chromosome. In contrast to the west-type, the east-type karyotype (Fig. 2B) possessed 13 pairs of M elements (nos. 1–12 and 14) and two pairs of SM elements (nos. 15 and 16) in autosomes, although the other karyotypic features were almost equal to those of the western. Accordingly, the latter karyotype had one more pair of large M elements and one fewer pair of large ST elements than the former. As shown in Fig. 2, the chromosomal variation was due to the pair no. 14 which was classified as subtelocentric in the west-type karyotype and as metacentric in the east-type one.

On the basis of the dimorphism in no. 14 autosomal pair, the specimens examined here were divided into two groups (Fig. 1). One group having the west-type karyotype (ST pair no. 14)(Fig. 2A) contained 161 individuals obtained from 36 localities in western Japan, so the group was designated as "the western race". The other group having the east-type karyotype (M pair no. 14) (Fig. 2B) included 84 specimens from 21 localities in eastern Japan, so the group was designated as "the eastern race".

G- and C-banding

Fig. 3 shows a typical G-banded karyotype for each race. In either race, the chromosomes were well segmented, and consequently all autosomal homologues could be precisely identified by their G-band patterns. The X chromosomes of both the western and eastern races were also well segmented. The comparison of the G-banded karyotype between the two races are mentioned later.

As shown in Fig. 4, the C-band technique produced similar banding patterns to each other, although a slight variation was found in the size of C-band in some pairs between the two races. In both races, the X chromosome had a large amount of constitutive heterochromatin on the proximal two-thirds of its short arm. Most of chromosomes in both races possessed centromeric and telomeric C-bands, but intensities of these C-bands were moderate or faint depending on each chromosome. Pericentromeric C-bands of no. 1 in the eastern race were slightly larger than those of no. 1 in the western race, although no obvious difference was found in their G-band patterns between the races (see Fig. 5). The pair no. 14 of the western race had centromeric C-bands together with indistinct pericentromeric bands, while that of the eastern race lacked centromeric C-band, but the long arms were C-band positive along its proximal one-third.

Pair-matching of the G-banded karyotype between the two races

To clarify the mechanism of chromosomal changes in *U. talpoides*, we pair-matched the G-band patterns of the western and eastern races (Fig. 5). There was a partial mismatching in no. 14 element between the western and eastern races, although the G-banding patterns of all the other chromosomes were highly homologous between the two races. Pair no. 14 of chromosomes were almost same in size, but they had different G-band patterns. As schematically shown in Fig. 6, the structural variation between the two chromosomes could be well explained by assuming pericentric inversion, by which G-band pattern of pair no. 14 would become identical between the two races.

DISCUSSION

Results of this study based on many specimens from different sampling localities show that the greater Japanese shrew-mole, *Urotrichus talpoides*, consists of two karyotypic races distributing parapatrically in western and eastern Japan. Our observations also demonstrate that these two karyotypic races have a boundary running through the central part of Honshu from Kurobe in Toyama Prefecture to Fuji in Shizuoka Prefecture (see Fig. 1).

Karyotypic variation

The two races of *U. talpoides* are identical in their diploid chromosome number (2n=34), fundamental number (FN=64), and sex chromosome morphology. Our karyotypic findings are essentially consistent with those in earlier karyological studies (Tsuchiya and Yosida, 1971; Tsuchiya, 1979, 1987, 1988; Hamada and Yosida, 1980; Kawada and Obara, 1999). How-

Table 1. Localities and the numbers of *Urotrichus talpoides* examined. Locality numbers correspond to those in Fig. 1.

Locality number	Sampling locality	Number of specimens female	male	Month and year of collection
1	Nakayama, Kamiagata, Nagasaki Pref.	1	1	Nov. 1990
2	Wakasugiyama, Sasaguri, Fukuoka Pref.	2	3	Jun. 1988
3	Yufuin, Oita Pref.	0	1	Mar. 1992
4	Kurusonzan, Toyota, Yamaguchi Pref.	3	1	May 2000
5	Yumoto, Nagato, Yamaguchi Pref.	2	2	Dec. 1989
6	Sakurayama, Mine, Yamaguchi Pref.	1	1	Apr. 2000
7	Kagamino, Tomata, Okayama Pref.	5	3	Apr. 1990
8	Ishizuchi, Omogo, Ehime Pref.	3	4	Oct. 1992
9	Minokoshi, Tsurugi, Tokushima Pref.	6	7	May 2000
10	Hirai, Kozagawa, Wakayama Prep.	0	1	Jul. 1992
11	Nachisan, Nachikatsuura, Wakayama Pref.	3	4	Mar. 1989
12	Yunomene, Higasimuro, Wakayama Pref.	0	2	Mar. 1989
13	Odaigahara, Kamikitayama, Nara Pref.	6	10	May 1989
14	Wasamatayama, Kamikitayama, Nara Pref.	4	6	Nov. 1992
15	Oji, Kitakatsuragi, Nara Pref.	0	1	Jul. 1992
		2	1	May 1999
		2	0	Feb. 2000
16	Murou, Uda, Nara Pref.	1	1	Jun. 1990
17	Moriyama, Shigacho, Shiga Pref.	1	0	Feb. 1989
18	Seto, Aichi Pref.	2	1	Feb. 1989
19	Mitake, Kani, Gifu Pref.	1	4	Apr. 1989
20	Toyooka, Iwata, Shizuoka Pref.	2	0	Apr. 1990
21	Okubo, Mori, Shizuoka Pref.	4	2	Apr. 1990
22	Sumatakyo, Motokawane, Shizuoka Pref.	2	2	Apr. 1990
23	Tomisawa, Yamanashi Pref.	2	0	May 1999
24	Shinno, Anan, Nagano Pref.	0	2	Nov. 1983
25	Iida, Nagano Pref.	0	1	Jun. 1983
26	Komagane, Nagano Pref.	1	3	Oct. 1989
27	Osaka, Masuda, Gifu Pref.	1	2	Nov. 1983
28	Nakao, Kamitakara, Gifu Pref.	4	2	Aug. 1989
29	Azumimura, Nagano Pref.	0	1	Aug. 1989
30	Shiramine, Ishikawa Pref.	4	3	Oct. 1991
31	Ichirino, Oguchi, Ishikawa Pref.	4	2	May 1988
32	Shirakawagou, Gifu Pref.	0	3	Nov. 1998
33	Ainokura, Tairamura, Toyama Pref.	1	3	Nov. 1989
34	Awasuno, Tateyama, Toyama Pref.	0	1	Nov. 1989
35	Uchiyama, Unazuki, Toyama Pref.	0	1	Nov. 1989
36	Wajima, Ishikawa Pref.	2	7	Nov. 1990
37	Hashiba, Unazuki, Toyama Pref.	1	1	Nov. 1989
38	Ogawamotoyu, Asahi, Toyama Pref.	0	2	Nov. 1988
39	Tsubame, Niigata Pref.	0	4	May 1998
40	Tsugaike, Otari, Nagano Pref.	1	2	May 1986
41	Hakuba, Nagano Pref.	0	1	May 1986
42	Omachi, Nagano Pref.	1	0	Oct. 1989
		3	2	May 1998
43	Azusagawamura, Nagano Pref.	1	1	Sep. 1996
44	Utsukushigahara, Nagano Pref.	1	0	May 1998
45	Tsumagoi, Gunma Pref.	0	1	Jun. 1992
46	Kisofukushima, Nagano Pref.	1	0	Dec. 1999
47	Yanagisawa, Ina, Nagano Pref.	6	13	Oct. 1989
		0	1	Dec. 1998
48	Takato, Nagano Pref.	1	1	Oct. 1988
49	Ashiyasuonsen, Yamanashi Pref.	5	4	May 1999
50	Shosenkyo, Yamanashi Pref.	1	3	May 1999
51	Minobu, Yamanashi Pref.	4	0	May 1999
52	Shimobeonsen, Yamanashi Pref.	1	1	May 1999
53	Narusawamura, Yamanashi Pref.	1	0	Sep. 1984
54	Kamisano, Nanbu, Yamanashi Pref.	2	4	Mar. 1990
55	Yugashima, Amagi, Shizuoka Pref.	7	2	Mar. 1990
56	Asahimura, Higashitagawa, Yamagata Pref.	2	1	Jul. 1990
57	Tenmabayashi, Kamikita, Aomori Pref.	0	1	Aug. 1997
	Total	111	134	

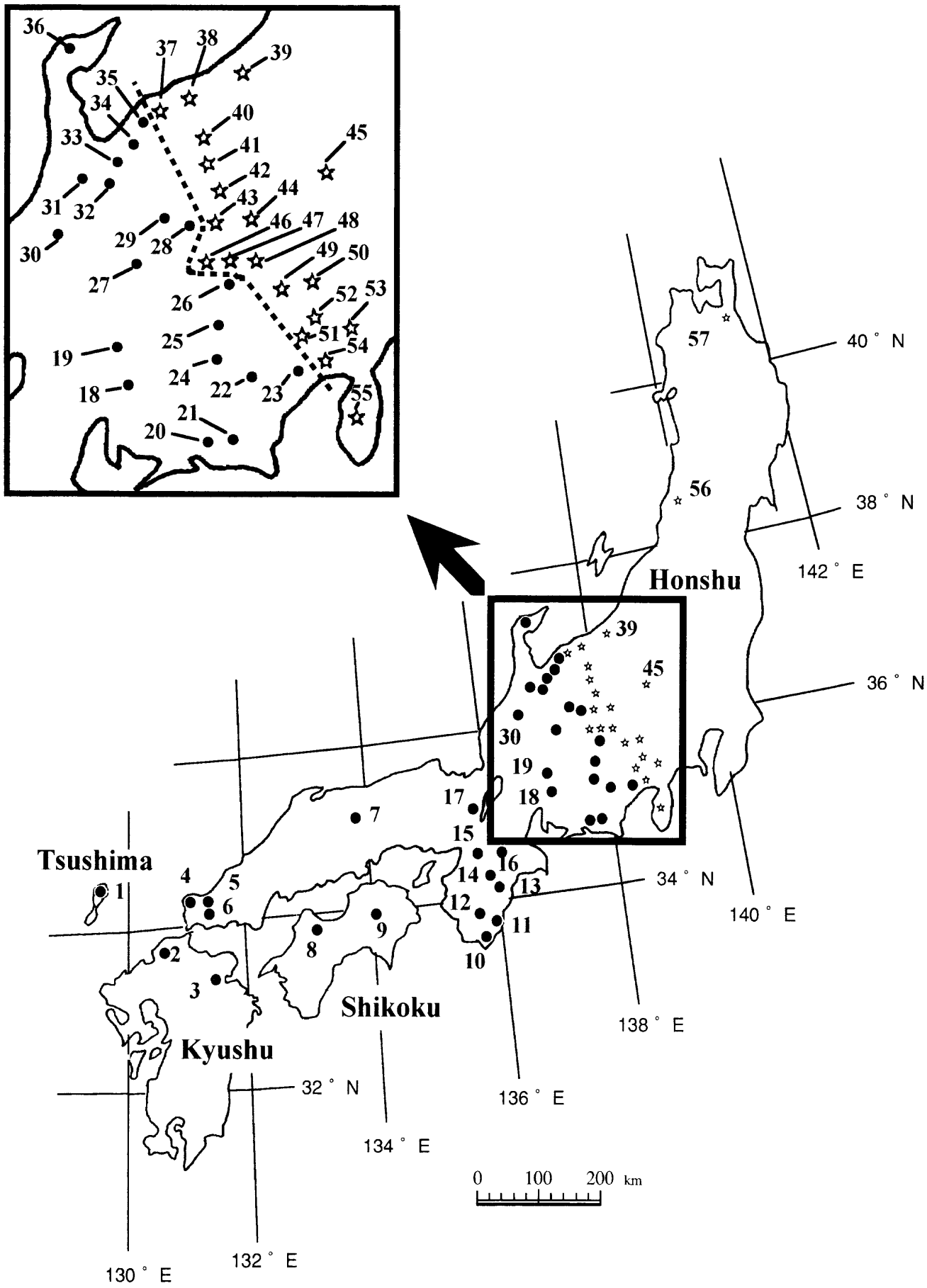

Fig. 1. Map showing 57 localities where specimens with the western karyotype (solid circles) and with the eastern karyotype (open stars) were collected. The locality numbers correspond to those in Table 1. A broken line in central Honshu represents the boundary between the western race and the eastern race of *Urotrichus talpoides*.

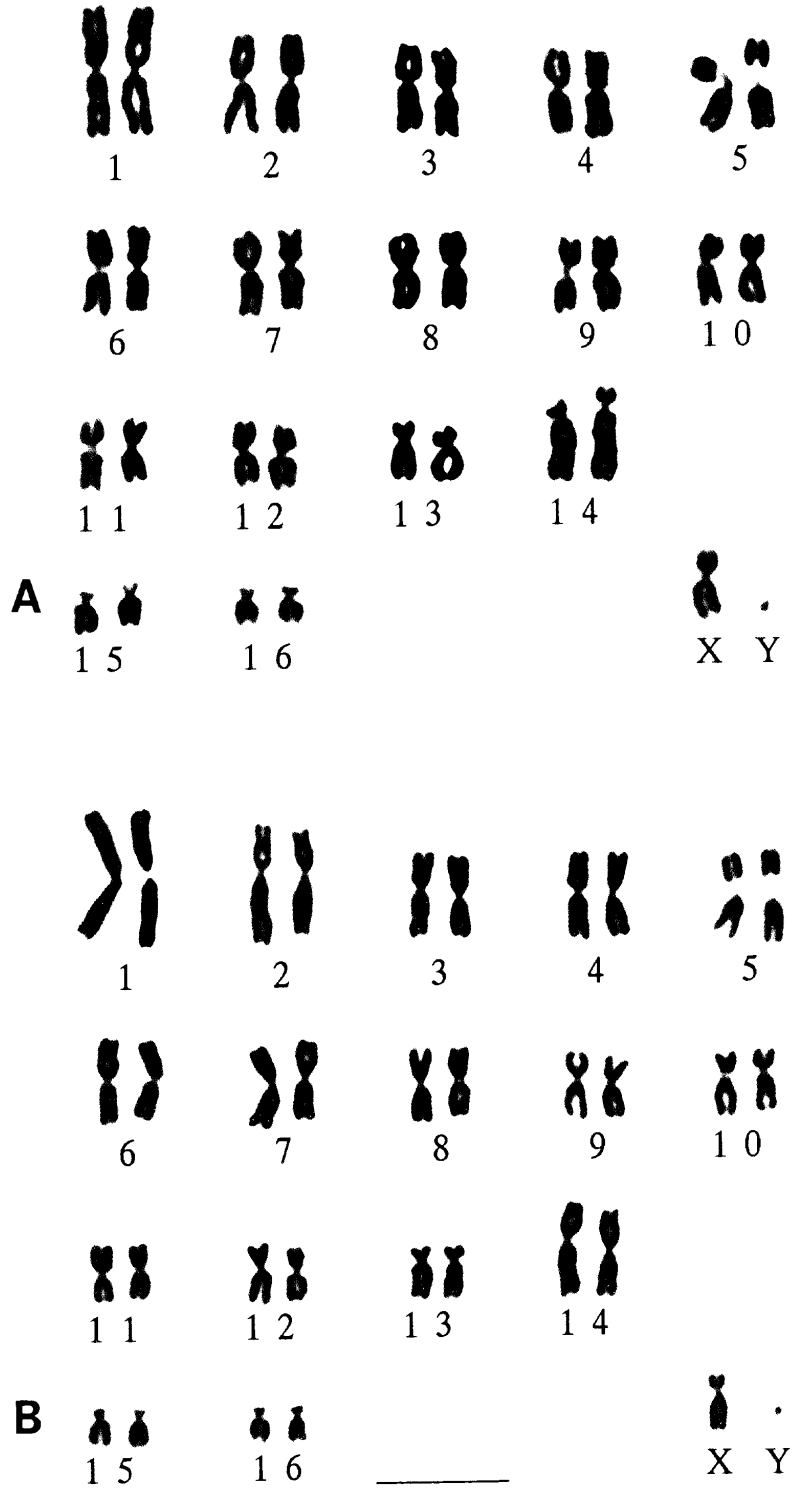

Fig. 2. Conventional karyotypes of the western race (A) and eastern race (B) of *Urotrichus talpoides*. Bar=10 μm.

ever, in the conventional karyotype, the two races have chromosomes with different makeups. The 34 chromosomes of the western race were composed of 12 M pairs, one SM pair and three ST pairs of autosomes, with a medium-sized M X chromosome and a dot-like Y chromosome. On the other hand, the eastern race had one extra pair of M elements and lacked one pair of ST elements, compared with the western race. In other words the no. 14 autosomal pair was classified as subtelocentric in the western race and as metacentric in the eastern race. Our results confirmed the karyotypic features of the chromosomal variants in eastern Honshu referred to by Tsuchiya (1987, 1988). Furthermore, our G-band analysis revealed that pericentric inversion is responsible for morphological change found in no. 14 autosomal pair. The comparison of C-band patterns suggested that nos. 1 and 14 pairs exhibited slight variation in the amount of constitutive (C) heterochromatin. In the autosomal pair no. 14, the chromosomal variation appears to be involved in not only pericentric inversion but also quantitative alteration of C-heterochromatin without change of chromosome size.

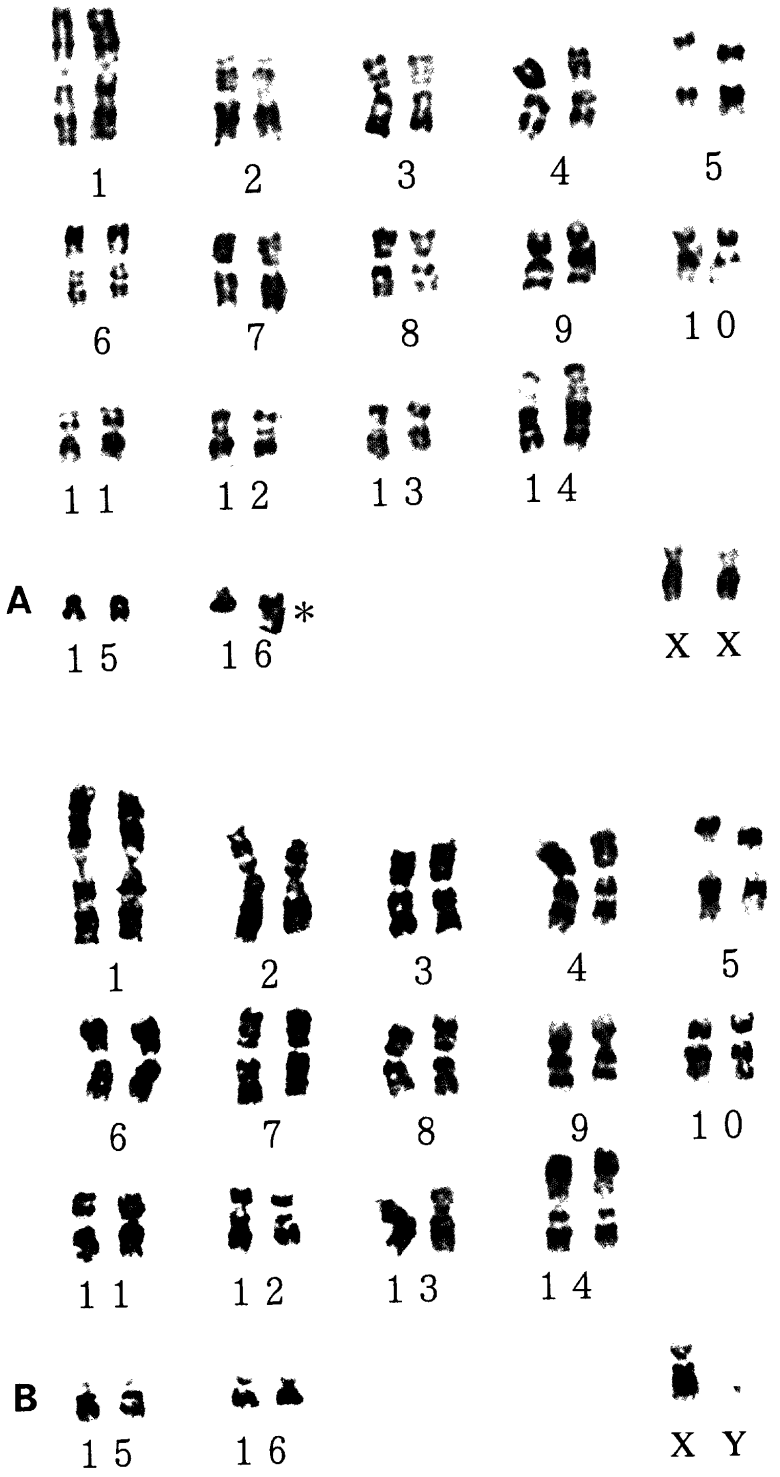

Fig. 3. G-banded karyotypes of the western race (A) and eastern race (B) of *Urotorichus talpoides*. An asterisk indicates overlapping chromosomes.

Inquiring into the direction of chromosomal changes within a group of organisms, it is important to consider karyotypes of their sister group. It is generally accepted that the lesser Japanese shrew-mole, *Dymecodon pilirostris*, found in relatively high mountains of Honshu, Shikoku and Kyushu (Imaizumi, 1970; Abe, 1994) is a closest relative to *U. talpoides* and is more primitive than *U. talpoides* on the basis of the usual taxonomic criteria such as dental and skull systems. The conventional karyotype of the western race of *U. talpoides* is almostidentical with that of *D. pilirostris*, both of which are characterized by ST pair no. 14 (Harada and Ando, unpublished data). Moreover, the western race of *U. talpoides* and *D. pilirostris* show almost perfect G-band homology (Hamada and Yosida, 1980; Harada and Ando, unpublished data). Our C-band pattern of no. 14 chromosomes in the western race of *U. talpoides* is quite similar to that in *D. pilirostris* presented by Kawada and Obara (1999). Considering the fact that *U. talpoides* is divided into two karyotypically different races, coupled with the great similarities in karyotype between the western race of *U. talpoides* and *D. pilirostris*, it is inferred

Fig. 4. C-banded karyotypes of the western race (A) and eastern race (B) of *Urotorichus talpoides.*

that the karyological events, i.e. pericentric inversion and quantitative change of C-heterochromatin, in the pair no. 14 of *U. talpoides* might have occurred after speciation in the common ancestor of *U. talpoides* and *D. pilirostris*, and that the western race might have preserved the original karyotype of *U. talpoides*. The similar inference has been drawn by Kawada and Obara (1999).

Members of the family Talpidae have been found to exhibit a remarkable degree of chromosomal conservatism and intraspecific euchromatic chromosomal variation has not been reported yet in this taxon (Yates and Moore, 1990). Reumer and Meylan (1986), however, listed *Talpa romana* as the species in which chromosomal variation due to pericentric inversion was found in a chromosome. They also noted a heterochromatic polymorphism in *Scalopus aquaticus*. In the present study, we revealed that the pericentric inversion and quantitative change of C-heterochromatin were responsible for the karyotypic differentiation in *U. talpoides*. Intraspecific and geographical variation in chromosomes of *U. talpoides* caused by these events is rare and unique among the talpid

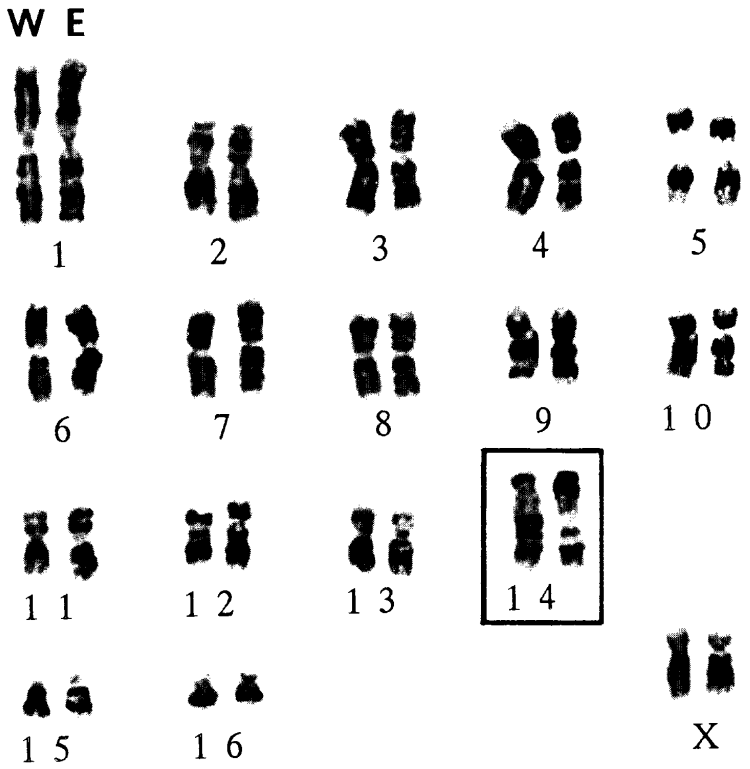

Fig. 5. Pair-matching of G-banded chromosomes between the western race (W) and the eastern race (E) of *Urotorichus talpoides*. The pair of mismatching chromosomes is enclosed in a rectangle frame.

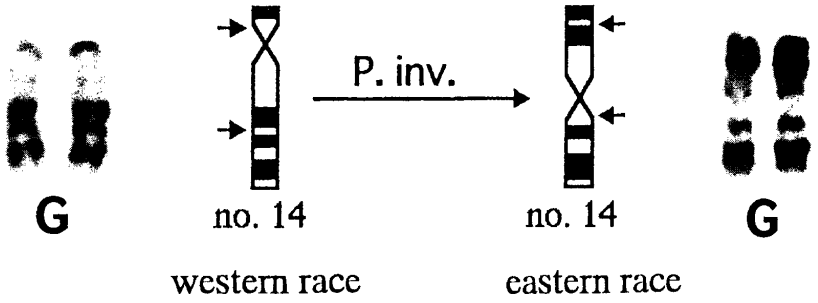

Fig. 6. Photograph and diagram of pericentric inversion between chromosomes no. 14 of the western race and the eastern race of *Urotrichus talpoides*. Short arrows indicate putative break points. The long arrow indicates a probable direction of chromosomal change. G, G-band staining: P. inv., pericentric inversion.

species examined so far. Nevertheless, our results also suggest that pericentric inversion and C-heterochromatin variation may play a role as one of the causes for karyotypic differentiation in Talpidae. Various modes of chromosomal rearrangements have been identified in the karyotypic differentiation and speciation in various lineages of mammals. As an example where intraspecific karyotypic variation has been much studied in other groups of Insectivora, several solicid species have been well known (Fredga, 1973; Searle, 1984 for the common shrew *Sorex araneus*; Yong, 1971, 1972; Andō *et al.*, 1980; Obara and Miyai, 1981; Yosida, 1982 for the Asian house shrew *Suncus murinus*; Ruedi and Vogel, 1995 for the Southeast Asian shrews *Crocidura* spp.; Elrod *et al.*, 1996 for the southern short-tailed shrew *Blarina carolinesis*). In these species, the karyotypic variations mainly involved Robertsonian rearrangements and changes in the amount and location of C-heterochromatin.

Geographical border between the two races and its implications

Tsuchiya (1987, 1988) suggested that the eastern population of *U. talpoides* may be characterized by a derivative karyotype, and suspected that the population ranges eastward from the isthmian line connecting the Owari area of Aichi Prefecture to Tsuruga in Fukui Prefecture. As clearly shown in Fig. 1, however, our results demonstrated that the boundary between the two karyotypic races is actually located along the Kurobe-Fuji line, but not along the isthmian line postulated by Tsuchiya (1987, 1988). A similar situation has been reported for the large Japanese field mouse, *Apodemus speciosus*, consisting of two Robertsonian chromosomal races characterized by 2n=48 and 2n=46 karyotypes which distribute parapatrically in the eastern and western parts of Japan, respectively, with a narrow hybrid zone along the Toyama (Toyama Prefecture)-Hamamatsu (Shizuoka Prefecture) line

(Tsuchiya *et al.*, 1973; Tsuchiya, 1974; Saitoh and Obara, 1986, 1988; Saitoh *et al.*, 1989), which seems to be contiguous to the Kurobe-Fuji line of *U. talpoides*. Heterozygotic specimens of *A. speciosus* with 2n=47 have been trapped only in this zone, about 5 to 20 km wide (Harada *et al.*, 1984). Such chromosomally heterozygotic individuals signify the existence of the contact zone between the two races that are reproductively compatible with each other. In *U. talpoides*, however, no heterozygotic specimen showing interbreeding between the two races has been captured in the vicinity of the possible border of the two races. This finding may suggest more advanced level of geographical isolation between the two races, as compared with the case of *Apodemus speciosus*. The absence of heterozygotes may imply their elimination due to hybrid disadvantage or breakdown. Crossbreeding experiments are necessary in this respect and additional chromosomal surveys might reveal hybrids if any would appear. Aside from the level of reproductive isolation, the contiguity of the boundary lines of *A. speciosus* and *U. talpoides* may give us a clue to solve a riddle for their geographical distribution.

Urotrichus is considered to be one of the oldest genera of moles in Japan (Kamei *et al.*, 1988). *Urotrichus talpoides* does not occur in Hokkaido, and does occur in Tsushima Island and the Goto Islands as well as Kyushu, Shikoku and Honshu (Imaizumi, 1970; Abe, 1994). This pattern of distribution suggests that the ancestral population of *U. talpoides* migrated into Japan from the Asian continent via wide land connections covering a southern route or the Korean Peninsula (Imaizumi, 1975). Considering this, as well as the parapatric distribution of the two races, a scenario could be hypothesized for the historical and zoogeographical processes of the divergence in *U. talpoides*. In the scenario, the west-type shrew-moles came into Japan first and then, the east-type shrew-moles arose from the former somewhere in the eastern part of Japan, gradually expanding geographically to occupy their present range eastward to the Kurobe-Fuji boundary line.

When testing a hypothesis for the process of divergence of a given species in islands off the coast of a continent, it is important to consider genetic information, which is obtained from, for example, biochemical allozyme analysis, on the species and the related species occurring in the continent, as in the case of Taiwanese rodents (Yu, 1995). The genus *Urotrichus* is endemic to Japan and no congener is distributed in the Eurasian continent. Only two monospecific genera (*Scaptonyx* and *Scapanulus*) belonging to the subfamily Scalopinae are found in inland areas of the Eurasian continent (Corbet and Hill, 1992). No karyological or phylogenetic information has been reported on these two continental genera. From currently available information on *U. talpoides*, it is uncertain whether our view is the case or not. However, if the scenario is actually the case, it is likely that the process of karyotypic differentiation in *U. talpoides* have progressed in a stasipatric mode (White, 1968; Wilson *et al.*, 1975) in eastern Honshu and the boundary plays a certain role for maintaining the parapatric distribution of the two races as in the case of *A. speciosus* (Saito and Obara, 1988). For *A. speciosus*, the karyological and biochemical studies have revealed that the 2=46-type race arose newly somewhere in the southern part of Japan after the ancestral form with 2n=48 came to Japan from the continent through the Korean Peninsula (Saitoh and Obara, 1986, 1988; Saitoh *et al.*, 1989). In *U. talpoides*, biochemical and molecular phylogenetic studies and comparative karyotypic studies will constitute the next step for the assessment of the degree of genetic differentiation and the process of divergence among the two races of *U. talpoides* and *D. pilirostris* in Japan and related taxa in the Eurasian continent.

ACKNOWLEDGMENTS

We thank Prof. K. Kondo, Prof. M. Yoshida, Dr. K. Ohno, Messrs. T. Hamada, K. Yachiguchi, S. Nishio and Mrs. S. Kato for their help in collecting specimens. We are grateful to Ms Caroline Latta, Osaka City University Medical School, for checking an earlier English draft, and to Dr. A. P. Kryukov, Institute of Biology and Soil Science, Far East Division of the Russian Academy of Sciences and anonymouse referees for valuable comments on the manuscript. This work was supported in part by a Grant-in-Aid for Cooperative Research from the Ministry of Education, Science, Sports, and Culture, Japan.

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(Received December 6, 2000 / Accepted January 10, 2001)