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ORIGINAL PAPER

Dental anomalies in the Japanese mole *Mogera wogura* from northeast China and the Primorsky region of Russia

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Abstract Dental anomalies in the Japanese mole, *Mogera wogura* Temminck, 1842, from northeast China and the Primorsky region of Russia were examined based on 241 specimens. The most frequent dental anomaly was oligodonty, i.e., missing P^2 (18 cases) or P_3 (one case). Supernumerary teeth were observed in three cases, two of which were characterized by abnormal shapes. Morphological abnormalities in teeth (six cases) and an asymmetrically curved rostrum (one case) were also observed. Dental anomalies were found at higher frequencies in populations near the northern range limit of the species. This was not caused by size effects. We suggest that the high incidence of dental anomalies was the result of genetic drift, which increases in marginal populations. Considering the nature of subterranean mammals, our results suggest that the high frequency of dental anomalies in a marginal population could have initiated the evolution of dental formulae if parapatric or peripatric speciation occurs in such populations.

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Introduction

Individual dental anomalies, that is, numerical or morphological abnormalities have been documented in several species of moles in Talpini (Soricomorpha: Talpidae) (Ueda 1959; Ziegler 1971; Abe et al. 1991; Krystufek et al. 2001; Motokawa et al. 2001; Kawada et al. 2006). Oligodonty has been observed most frequently, and the missing teeth are often identified as upper second premolar (P^2; upper teeth indicated by a superscript number hereafter), lower third incisors (I_3; lower teeth indicated by subscript number hereafter), or P_2. These three teeth are also involved in differences in dental formula among genera in this clade (Ziegler 1971; Kawada 2005). Additionally, some species have completely lost several teeth compared with the closest species. For example, *Mogera uchidai* lost P^2 and P_2 from its closest relative, *Mogera insularis* (Abe et al. 1991; Motokawa et al. 2001). In mammals, individual dental anomalies, particularly oligodonty, are often observed in taxa in which teeth number tends to decrease (Ohtaishi 1986). Therefore, the occurrence of dental anomalies could depict the evolutionary mechanism of teeth number, i.e., dental formulae. In this study, we examined dental anomalies in the Japanese mole, *Mogera wogura*, from northeast China and the Primorsky region of Russia. *M. wogura* is distributed in Japan, Korea, the Primorsky region of Russia, and northeast China (Hutterer 2005), although some authors consider the Russian and Chinese populations surveyed in this study to form a separate species *Mogera robusta* Nehring, 1891 (Pavlinov et al. 1995; Zhang 1997;

Pan et al. 2007; Hoffmann and Lunde 2008). We discuss the geographic differences in the patterns and rates of dental anomalies.

Materials and methods

We examined 241 skulls at the Institute of Biology and Soil Science, Russian Academy of Sciences, Vladivostok, Russia (AK; n=48); the Zoological Museum of Moscow State University, Moscow, Russia (MU; n=188); and Yamashina Institute for Ornithology, Abiko, Japan (YIO; n=5). These specimens were collected from eight localities (Fig. 1): Sikhote-Alin Reserve (n=30), Lazo Reserve (n=38), Ussuri district (n=86), Vladivostok city suburbs (n=7), Hasan district (n=66), Harbin (n=12), Jilin (n=1), and Mudanjiang (n=1).

We examined dentition under a microscope (magnification range, ×10–20). A supernumerary tooth (polydonty) was defined as an extra tooth without any fusion in the crown or root, whereas oligodonty was defined as the absence of a tooth without evidence of concrescence. We measured three cranial variables on each skull to ±0.1 mm: the greatest length of the skull from the anterior end of the palate to the end of the cranium (greatest length of skull, GLS), palatal length from the anterior tip of the first incisor to the posterior lip of the palate (PL), and the distance from the anterior tip of the canine to the posterior tip of the third upper molar (CM3). Age in years was determined by the degree of tooth attrition following the criteria of Okhotina (1966). Briefly, teeth of moles younger than 1 year are not worn, those of 1-year olds are visibly worn, and those of 2-year olds are worn more and have lost the sharpness in all cusps of all molars. Subsequently, we estimated age in months for specimens less than 1 year old as the time from June to the month of collection because the birth season for *M. wogura* on the continent is May–June (Pan et al. 2007) or May–July (Okhotina 1966).

Results

Among 241 specimens, 217 had normal dentition (Fig. 2) whereas 24 possessed dental anomalies: 19 with oligodonty, three with supernumerary teeth, and four with abnormally shaped teeth, including two specimens with abnormally shaped supernumerary teeth (Table 1). In addition to these anomalies, we found one abnormal skull (MU #76805 from the Ussuri district) with normal dentition whose rostrum anterior to P^4 was asymmetric and curved to the left side (to the upper side of the photo; Fig. 3).

Of 19 cases of missing teeth, 18 were missing P^2 in the upper dentition on the right, left, or both sides (Fig. 4) whereas the remaining case (MU #41280 from Lazo Reserve) was missing a left lower P_3 (MU #41280, Fig. 5). P^2 was missing more often from the right than from the left side (17 vs. five cases, respectively; Fisher's exact test, p=0.015).

Supernumerary and/or abnormally shaped teeth were found in five specimens (see below). Supernumerary teeth in AK #605 from Hasan were expressed as two teeth between P^1 and P^3, both of which were similar in height, length, and width to a normal P^2; however, the mesial and distal tubercles of the distal tooth were better developed

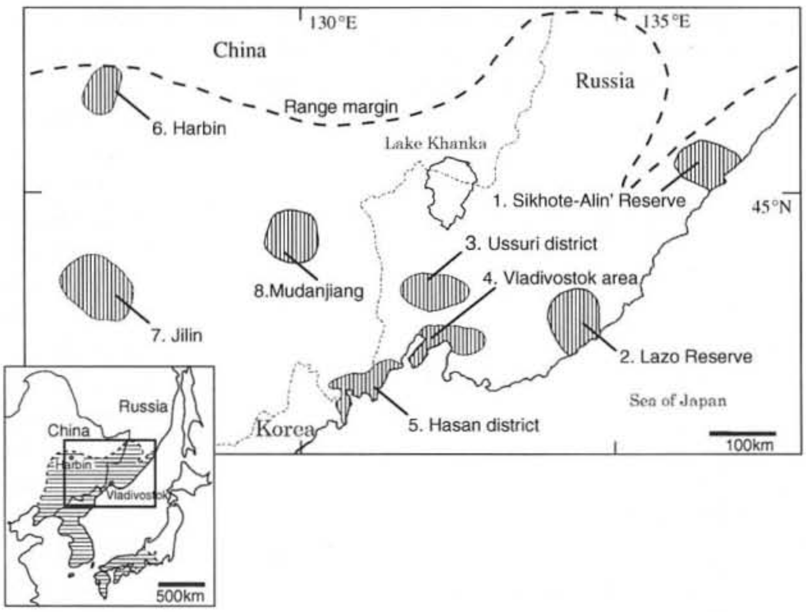

Fig. 1 Map of northeast China and the Primorsky region of Russia showing specimen localities (*vertical line*) with the entire *M. wogura* distribution range (*horizontal line*) following Okhotina (1966), Zhang (1997), and Hoffmann and Lunde (2008)

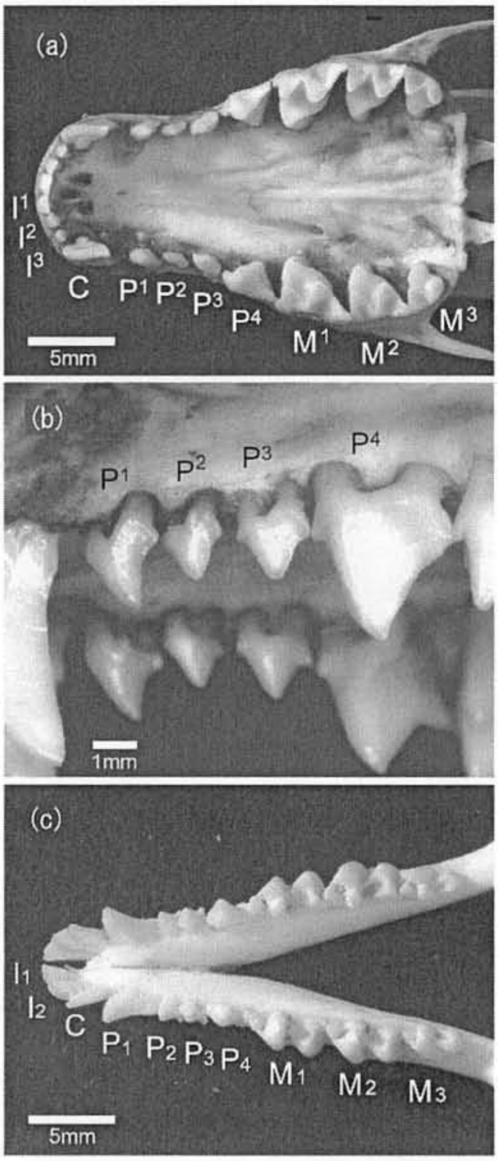

Fig. 2 Normal dentition of *M. wogura*: occlusal view of the upper dentition (**a** AK #1125 from Sikhote-Alin Reserve), labial view of the left upper premolars (**b** AK #608 from the Hasan district), and occlusal view of the lower dentition (**c** AK #41 from Sikhote-Alin Reserve)

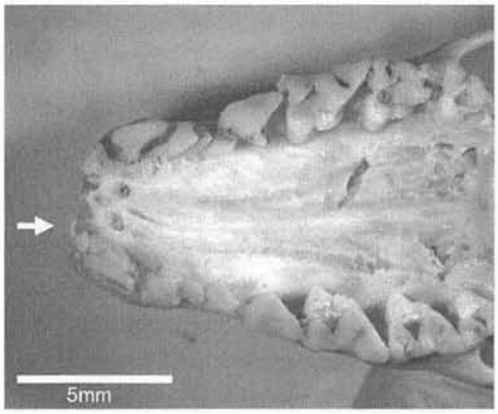

Fig. 3 Ventral view of an abnormal skull with a rostrum curved to the left side (MU #76805 from the Ussuri district)

than those of the mesial tooth (Fig. 6). That is, the tubercles were higher and broader in the distal tooth (Fig. 6).

A supernumerary and abnormally shaped tooth was found in one specimen (AK #706 from Hasan) between the normal-shaped P^2 and P^3 in the left upper dentition (Fig. 7). This tooth was similar in height to P^2. The mesial and distal tubercles were both oriented to the buccal side with the roots, and the distal tubercle was more developed than the mesial one, forming a metastyle similar to a normal P^2.

Two small, single-rooted teeth were found in one specimen (AK #002 from Vladivostok) at the P_3 position in the right lower dentition and this was also a case of a supernumerary tooth (Fig. 8). These erupted teeth were at the positions of the two roots for a normal P_3 and covered with enamel, with incompletely constructed main cusps and mesial and distal tubercles with small metastyles. The smaller and anterior tooth erupted on the lingual side of the larger and posterior tooth. On the opposite (left) side of the P_3 in the same specimen, we observed two remnant roots but could not determine whether they were independent. An abnormally small M_3 was found in the left lower dentition

Table 1 Cases of dental anomalies in different populations of *M. wogura*: abnormal individuals, oligodonty, missing P^2 (left side/both sides/right side) or P_3, supernumerary teeth in the upper premolar series or lower premolar series, and morphological abnormalities

Locality	Number	Abnormal individuals (%)	Oligodonty (N=19)		Supernumerary (N=3)		Morphological abnormality (N=6)
			P^2	P^3	Upper P	Lower P	
Sikhote-Alin Reserve	30	7 (23.3%)	7 (0/2/5)				
Lazo Reserve	38	2 (5.2%)	1 (0/0/1)	1			
Ussuri district	86	6 (6.9%)	4 (0/1/3)				2
Vladivostok area	7	1 (14.2%)				1	3
Hasan district	66	3 (4.5%)	1 (0/0/1)		2		1
Harbin	12	5 (41.6%)	5 (1/1/3)				
Jilin	1	0 (0%)					
Mudanjiang	1	0 (0%)					
Total	241	24 (9.9%)	18 (1/4/13)	1	2	1	6

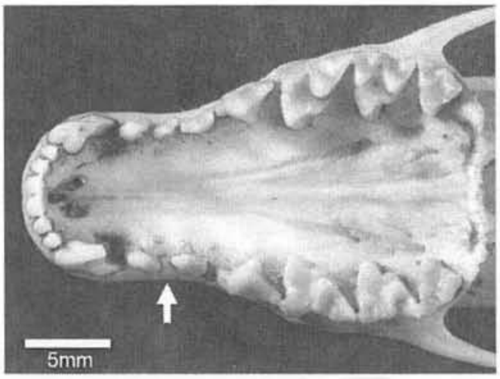

Fig. 4 Occlusal view of a case of oligodonty in which P^2 was missing (indicated by an *arrow*) in the right upper dentition (AK #904 from the Ussuri district)

of the same specimen. The tooth was small, single cusped, and located behind M_2 with a gap. Its length, height, and width were about one third that of a normal M_3, and the mesial part was higher than the distal part (Fig. 8).

An abnormally small P^2 was found in one specimen (MU #76848 from the Ussuri district) in the right upper dentition (Fig. 9). This abnormal tooth was single cusped, without mesial or distal tubercles, and shortened mesiodistally.

We observed only one root alveolus in a P^2 of the left upper dentition in a specimen (AK #19 from the Ussuri district), but we could not examine the tooth root directly because it was lost.

Rates of abnormal dentition did not differ between sexes (Fisher's exact test, $p=0.387$) but differed across localities ($p<0.05$). The rate of dental anomalies was higher in the Sikhote-Alin Reserve (23.3%) than in the Ussuri (6.9%) and Hasan districts (4.5%) and higher in Harbin (41.6%) than in the Ussuri and Hasan districts and Lazo Reserve (5.2%) (Fisher's exact test, $p<0.01$) (Table 1).

Three skull measurements from seven localities using specimens >6 months old are presented in Table 2. Moles

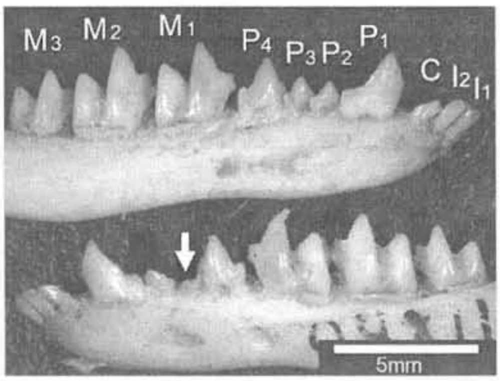

Fig. 5 Labial views of the normal right lower dentition (*top*) and a left lower dentition that is missing P_3 (*bottom*) (MU #41280 from Lazo Reserve)

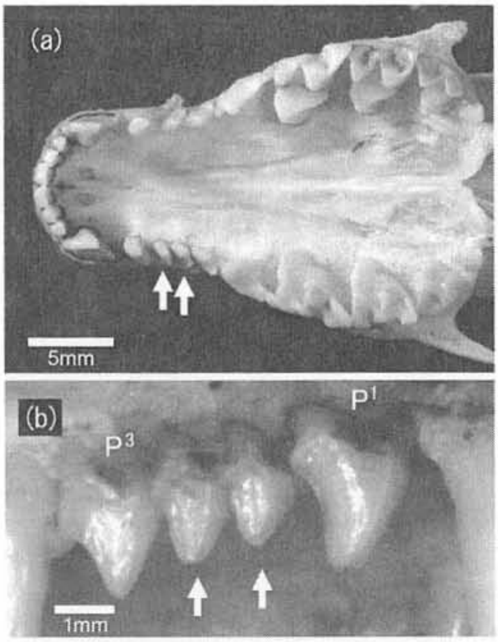

Fig. 6 Occlusal (**a**) and labial (**b**) views of duplicated teeth between P^1 and P^3 (indicated by *arrows*) in the right upper premolar series (AK #605 from the Hasan district)

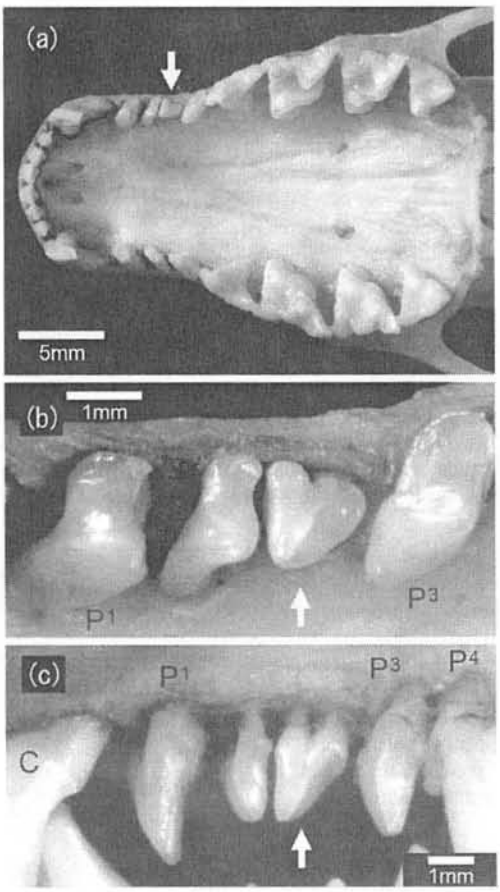

Fig. 7 Occlusal (**a**, **b**) and labial (**c**) views of a supernumerary tooth between P^1 and P^3 (indicated by *arrows*) in the left upper premolar series (AK #706 from the Hasan district)

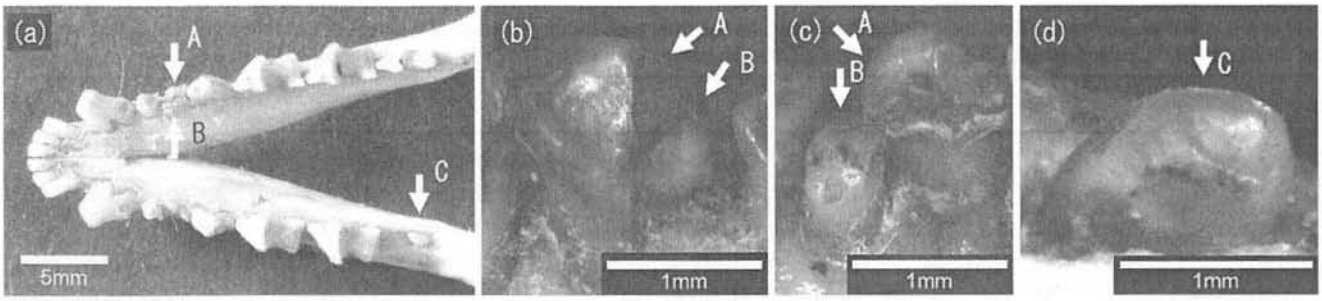

Fig. 8 Occlusal (**a**), labial (**b**), and lingual (**c**) views of two small teeth to the right of P_3 (indicated by *arrows A* and *B*) and lingual view of a small, single-cusped M_3 (**d**) (indicated by *arrow C*) (AK #002 from the Vladivostok area)

from the Ussuri district were larger than those from any other population, and those from Hasan were the smallest in all measurements for both sexes, although not all pairs differed significantly (ANOVA/Tukey's test, Ussuri district vs. Hasan males for GLS, PL, and CM3, $p<0.001$; Ussuri district vs. Sikhote-Alin Reserve males for GLS, $p<0.01$; Hasan vs. Sikhote-Alin Reserve females for GLS, $p<0.05$) (Table 2).

Discussion

Dental anomalies in *M. wogura* included oligodonty, supernumerary teeth, and abnormal morphology and were found mainly in the loci of P^2, P_3, and M_3. Previous studies have reported that a missing P^2 was the most frequent dental anomaly and a missing P_2 was the second most frequent anomaly in *M. wogura* based on specimens from Japan and Korea (Ueda 1959; Abe et al. 1991; Kawada et al. 2011). Our results from northeast China and the Primorsky region of Russia indicated that cases of a missing P^2 were also the most frequent, whereas no case of a missing P_2 was found among the 241 specimens examined.

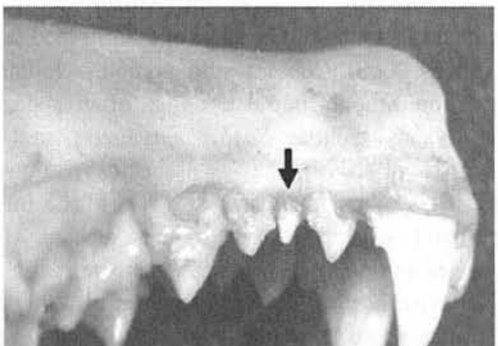

Fig. 9 Labial view of an abnormally small P^2 in the right upper dentition (MU #76848 from the Ussuri district)

We found several supernumerary teeth and morphological abnormalities that have not been reported previously. That is, supernumerary premolars, two small teeth erupted at the P_3 position and small, single-cusped tooth at the M_3 position, abnormally small P^2, and only one alveolus for P^2. The two similar teeth between P^1 and P^3 are likely similar to the "duplicated teeth" between P^1 and P^3 reported by Ueda (1959). In contrast, the supernumerary premolar seemed to be a duplicated P^2, whose anterior part rotated to the buccal side. This supernumerary tooth was reminiscent of the chisel-like supernumerary premolar teeth reported in *Talpa altaica* (Kawada et al. 2006), but in our case, the neck was folded and not cylindrical as in *T. altaica* (Fig. 7). The two small teeth at the P_3 position appeared as an independent tooth structure but erupted at the positions of the roots of P_3. The two teeth might have originated from the splitting of a tooth germ, as Wolsan (1984) categorized.

We observed 19 individuals with oligodonty as well as five with other kinds of dental anomalies. The latter cases differed from each other in type of anomaly, and we considered them rare. We discuss the different rates of dental anomalies among regions by combining all types of dental anomalies together.

Specimens from Sikhote-Alin Reserve and Harbin showed a high rate of dental anomalies relative to the other localities in this study as well as in previous studies on *M. wogura* from Japan (6.7% (n=119), Ueda 1959 and 6.43% (n=684), Kawada et al. 2011), and in Japan and Korea (2.8% (n=458), Abe et al. 1991). Some insignificant pairwise differences may have resulted from the small sample sizes, but all pairs with large sample sizes were significantly different. Thus, dental anomalies occurred more frequently in the Sikhote-Alin Reserve and Harbin populations. These populations are located near the northern range of this species (Okhotina 1966; Zhang 1997; Hoffmann and Lunde 2008) and are, thus, considered marginal populations (Fig. 1). Krystufek et al. (2001) reported the complete loss of I_3, P^2, and P_2 in a marginal population of *Talpa davidiana* (Talpini), and Szuma (2007) reported higher rates of M_3 absence in populations at the

Table 2 Cranial measurements from moles more than 6 months old from each locality (means±SD, ranges in parentheses) for the greatest length of the skull (GLS), palatal length (PL), and the distance from the canine to the third molar in upper dentition (CM3)

Locality	Sex	*N*	GLS	PL	CM3
Sikhote-Alin Reserve	M	9	43.39±1.15 (41.30–44.60)	16.90±0.45 (15.90–17.30)	16.13±0.56 (15.20–16.94)
	F	2	41.45±0.49 (41.10–41.80)	15.95±0.21 (15.80–16.10)	15.26±0.08 (15.20–15.32)
Lazo Reserve	M	6	43.32±0.63 (42.50–44.00)	17.07±0.85 (15.40–17.85)	15.94±0.28 (15.60–16.38)
	F	8	41.45±0.67 (40.49–42.55)	16.57±0.30 (16.00–16.91)	15.34±0.28 (14.67–15.54)
Ussuri district	M	34	44.84±1.11 (41.96–46.70)	17.31±0.51 (15.89–18.03)	16.35±0.47 (15.30–17.25)
	F	20	42.41±1.33 (38.89–45.20)	16.50±0.75 (13.84–17.14)	15.44±0.59 (13.31–16.43)
Vladivostok area	M	2	43.79±0.81 (43.22–44.37)	16.90±0.10 (16.83–16.98)	16.35±0.12 (16.26–16.44)
	F	1	41.60	16.20	15.28
Hasan district	M	26	43.27±1.48 (39.15–45.60)	16.59±0.68 (15.16–17.90)	15.75±0.55 (14.47–16.62)
	F	13	41.07±0.92 (39.43–43.40)	15.75±0.39 (15.20–16.70)	15.05±0.37 (14.46–15.87)
Harbin	M	4	43.59±1.53 (41.30–44.46)	16.94±0.55 (16.40–17.70)	15.96±0.48 (15.50–16.45)
Mudanjiang	M	1	44.46	16.99	16.45

northeastern and northwestern ends of the range of *Vulpes vulpes*. These results might suggest the tendency for increased rates of dental anomalies in mammals living in marginal populations.

Krystufek et al. (2001) stated that teeth loss in *T. davidiana* could be a byproduct of a reduction in skull size in a marginal population. A positive correlation between the rates of oligodonty and size reduction among populations has been reported in *Scapanus latimanus* (Hall 1940) and *M. wogura* in Japan (Kawada et al. 2011). In contrast, Szuma (2008) did not find a size reduction in populations with high rates of dental anomalies in *V. vulpes* in the range ends reported by Szuma (2007). In this study, reduced skull size was not observed in the Sikhote-Alin Reserve or Harbin populations (Table 2) and thus, the high rates of dental anomalies in these populations might not have been induced by a size effect.

Recent morphological and genetic studies in mammals concluded that oligodonty is caused by genetic factors rather than skull size in the cases of *Suncus murinus* (Jogahara et al. 2007), *V. vulpes* (Nentvichova and Andera 2008), blue terrier dogs (Knyazev et al. 2003), and mice (Line 2003). Furthermore, high incidences of dental anomalies have been reported in mammalian populations in which genetic drift is severe (Miles and Grigson 1990; Suchentrunk et al. 1992; Federoff and Nowak 1998; Martin 2007; Gomercic et al. 2009). Thus, the effect of genetic drift could be an important factor in the high rate of dental anomalies in the marginal populations of *M. wogura*.

Marginal populations have a typical demographic pattern characterized by low population density and fluctuating population size (Lomolino et al. 2005), leading to a small effective population size (Whitlock 2004). Theoretical studies have suggested that the effect of genetic drift is larger when effective population size is smaller (Futuyma 1998; Whitlock 2004). Actually, marginal populations have low genetic variation compared with central populations as a general tendency in wild animals and plants (Eckert et al. 2008; Kawecki 2008; Hardie and Hutchings 2010) and such examples have also been reported in mammals (Schwartz et al. 2003; Andersen et al. 2011). Thus, the effect of genetic drift may have increased in the marginal populations of *M. wogura*, and mutant alleles increased and induced dental anomalies.

Among 283 *M. wogura* study skins from the Primorsky region, only one specimen from Sikhote-Alin Reserve had a light yellowish skin instead of the common brown skin (A. Kryukov, personal observation; AK #727; deposited in the Botanical Garden Museum, Hokkaido University, Sapporo, Japan). We consider that this was an albino individual whose white skin was dyed with a secretion product and became yellow, as Yokohata (1997) reported for *M. wogura* from Japan. This albinism might also have been caused by rare mutations maintained in the marginal population by genetic drift.

Subterranean mammals often comprise parapatric populations, which have high levels of differentiation (Nevo 1999; Steinberg and Patton 2000) because of their limited dispersal ability (Lacey 2000). Consequently, complex chromosomal differentiation among populations is often reported in fossorial rodents such as *Spalax ehrenbergi* and *Spalax leucodon* (Nevo 1999), *Geomys* species (Smolen and Bickham 1994), and *Ctenomys* species (Massarini et al. 1991) as well as semi-fossorial rodents such as *Microtus maximowiczii* and *Microtus fortis* (Sheremetyeva et al. 2006, 2009; Kartavtseva et al. 2008; Frisman et al. 2009). Nevo (2001) distinguished four populations of *S. ehrenbergi* as new species with distinct karyotypes that were different from *S. ehrenbergi* and from each other: *Spalax galili*, *Spalax judaei*, *Spalax golani*, and *Spalax carneli*. Nevo (2001) concluded that the different karyotypes of these four species had been formed by genetic drift during each peripatric speciation event. Therefore, in other fossorial mammals, such as *Mogera* species, we suggest that a new diagnostic character such as a distinct karyotype could have been formed by genetic drift in newly established species from a marginal population through parapatric or peripatric speciation. If such a speciation event occurs in marginal populations where dental anomalies such as oligodonty are frequent, the anomalies could become a new dentition pattern with a different number of teeth. Therefore, we hypothesize that dental anomalies in marginal populations could have initiated the evolution of dental formulae in talpids and other subterranean mammals. Future studies of dental anomalies in marginal populations with more species should test this hypothesis.

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