Paleontological Research, vol. 13, no. 4, pp. 367–384, December 31, 2009

doi:10.2517/1342-8144-13.4.367

The middle Pleistocene Matsugae fauna, northern Kyushu, West Japan

SHINTARO OGINO[1], HIROYUKI OTSUKA[2] AND HIDEJI HARUNARI[3]

[1] *Geological Survey of Japan, National Institute of Advanced Industrial Science and Technology, Central7, 1-1-1 Higashi, Tsukuba, Ibaraki 305-8567, Japan (e-mail: ogino-s@aist.go.jp)*
[2] *The Kagoshima University Museum, Kagoshima University, Korimoto 1-21-35, Kagoshima City, Kagoshima 890-0065, Japan (e-mail: hmj4254@hyper.ocn.ne.jp)*
[3] *National Museum of Japanese History, Jonaicho 117, Sakura City, Chiba 285-8502, Japan (e-mail: haru@ybb.ne.jp)*

Received January 12, 2009; Revised manuscript accepted October 19, 2009

Abstract. The middle Pleistocene Matsugae mammalian fauna from the Matsugae limestone cave deposits in northern Kyushu, West Japan is reexamined based on the original fossil specimens and its biostratigraphical age is estimated. The Matsugae fauna includes 13 mammalian species representing 6 orders, 10 families and 12 genera that can be confirmed based on currently available fossil specimens. The taxa of the Matsugae fauna fall into four categories: the first encompasses a mammal that has been in existence since the early middle Pleistocene; the second comprises mammals that existed only during the middle middle Pleistocene; the third includes those that have specific characteristics of this age but may have a phyletic relationship to later Japanese mammals; and the fourth includes the direct ancestors of modern Japanese endemic species. The second and the third categories include several endemic taxa which are only known from this fauna. The mammalian fauna suggests an age referable to the Quaternary Mammal zone 4 (QM4), which is the middle part of the middle Pleistocene.

Key words: fauna, Japan, Mammalia, Matsugae, middle Pleistocene, migration

Introduction

The middle Pleistocene Matsugae limestone cave deposits in northern Kyushu, West Japan yielded many species of vertebrate fossils. Its mammalian assemblage, called the Matsugae fauna, was first collected and described by Tokunaga (1931) and then by Saito (1939) and Nobuo Naora (1944). These studies recognized 19 mammalian species. The specimens were stored in Waseda University, Tokyo, but some were broken or lost during World War II. In 1986, Hiroto Naora (son of Nobuo Naora) donated the specimens that were still extant to the National Museum of Japanese History (Sakura, Chiba, Japan). In this collection, 19 species of mammals were identified by Saito (1939) and Naora (1954, 1968). All of the specimens in this collection have now been placed in the "NAORA Nobuo Collection" of the National Museum of Japanese History (Harunari, 2008). Naora (1954) probably studied the Matsugae fauna using this "NAORA Nobuo Collection". Ogino and Otsuka (2005, 2008) have recently described macaque and mustelid fossils in this collection. The Matsugae fauna is important in terms of paleofaunal migration between Japan and the Asian Continent during the Pleistocene because records of the middle Pleistocene fauna in Japan are rare and among the Japanese Pleistocene faunas it is geographically located closest to the Asian Continent. However, the fauna was insufficiently described and discussed, so that its biostratigraphical zone remained unclear.

In this study, the fossil mammal specimens of the Matsugae fauna are reexamined. The purpose of this study is to revise and to clarify characteristics of the Matsugae fauna, and to determine the age of the fauna by comparison with other middle Pleistocene Japanese mammal faunas.

Geological setting

The Matsugae Cave occurs in the Permian limestones of the Akiyoshi Terrane (an accretionary complex), which is distributed in southwestern Japan (Nakae *et al.*, 1998). The cave was found in one of the limestone quarries in Kishi (Matsugae village, Moji-ku, Kitakyushu City, Fukuoka Prefecture, northern Kyushu, Japan (Figure 1), at the end of the

Table 1. Mammalian list of the Matsugae fauna.

Order	Genus and Species*	Genus and Species**	Specimen Number	Category
Rodentia	*Apodemus sylvatia speciosus*	*Apodemus speciosus*	NMJH-N0101 to NMJH-N0114	1
		Apodemus argenteus	NMJH-N0121 to NMJH-N0126	4
	Microtus montebelli montebelli	*Microtus epiratticepoides*	NMJH-N0131 to NMJH-N0139	3
Lagomorpha	*Lepus brachyurus brachyurus*	*Lepus* sp.	NMJH-N0141 and NMJH-N0142	3
Carnivora	*Canis alpinus*	—		
	Cuon sp. (Saito, 1939)	*Cuon* sp.	NMJH-N0151 and NMJH-N0152	2
	Lutra nipponica (Naora, 1968)	*Oriensictis nipponica*	NMJH-N0181 to NMJH-N0183	2
	Meles anakuma	—		
	Meles saheki	*Meles* sp.	NMJH-N0171	3
	Martes sp.	—		
	Mustela sp.	*Mustela itatsi*	NMJH-N0161 and NMJH-N0162	4
	Panthera sp.	*Panthera* sp.	NMJH-N0211 to NMJH-N0213	3
Cetartiodactyla	*Cervus nippon nippon*	*Cervus* sp.	NMJH-N0211 to NMJH-N0213	3
	Moschus sp.	—		
	Sus nipponicus	*Sus scrofa*	NMJH-N0251	3
	Proboselaphus sp.	—		
Perissodactyla	*Rhinoceros shindoi*	*Dicerorhinus* sp.	NMJH-N0201 to NMJH-N0203	2
Primates	*Macaca fuscata*	*Macaca* cf. *fuscata*	NMJH-N0241	3
Proboscidia	*Palaeoloxodon naumanni*	—		
	Stegodon sp.	—		

*Presented by Saito (1939) and Naora (1954 and 1968). **Stored at National Museum of Japanese History (this study).

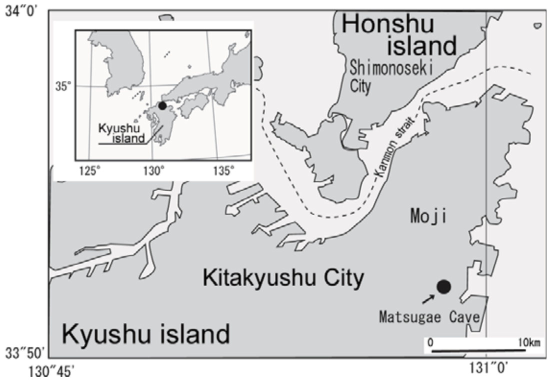


Figure 1. Location map of the Matsugae cave on the northern part of Kyushu Island, west Japan.

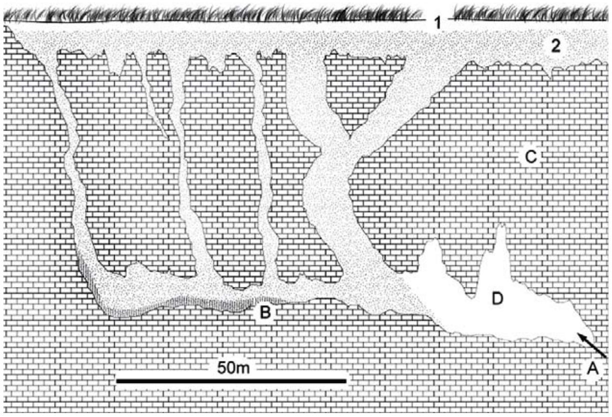


Figure 2. Diagram of the Matsugae cave (after Naora, 1954). **A**, entrance; **B**, fossil layers; **C**, limestone; **D**, the cavern hall; **1**, soil; **2**, red fissure deposit.

19th century. The mammal fossils were found in the Pleistocene deposits which had accumulated in the cave. The cave and cave deposits have since been removed by mining operations, the area is now residential. Naora (1954) presented a schematic diagram of the cave, based on information from a miner who worked at the old quarry (Figure 2). According to Naora (1954), the total length of the cave was estimated to be 100–120 m, with the entrance facing southeast (Figure 2A) Two fossiliferous layers were observed in the deposits: the first layer in the lower part of the cave and the second layer in the upper part of the cave (Figure 2B) The first layer overlay the second layer and consisted of a bone bed. The second, reddish brown layer consisted of chert conglomerates. All of the vertebrate specimens described in this paper were obtained from the first layer (Naora, 1999: appended by Harunari).

Materials and methods

The mammalian fossil specimens from the Matsugae cave previously studied by Naora (1954) are now stored in the National Museum of Japanese History (Sakura, Chiba, Japan)

Table 2. Dental measurements (in mm) of *Apodemus speciosus* and *Apodemus argenteus*.

Apodemus speciosus	**M1L**	**M1W**	**M2L**	**M2W**	**M3L**	**M3W**	**m1L**	**m1W**	**m2L**	**m2W**	**m3L**	**m3**
range	1.75 to 2.17	1.27 to 1.36	1.15	1.27	1.02	0.90	1.75 to 1.91	1.05 to 1.25	1.19 to 1.30	1.00 to 1.16	1.00	0.97
number	5		1		1		5		2		1.00	
average	1.96	1.33					1.82	1.13	1.20	1.08		
Apodemus argenteus	**M1L**	**M1W**	**M2L**	**M2W**	**M3L**	**M3W**	**m1L**	**m1W**	**m2L**	**m2W**	**m3L**	**m3**
range	-	-	1.1	0.89	0.75	0.79	1.49	0.96	1.00 to 1.08	0.80 to 0.87	0.72	0.59
number			1		1		1		3		1	
average									1.05	0.84		

under the catalogue name of the "NAORA Nobuo Collection". When the present study was initiated, the collection included *Lepus, Cuon, Meles, Oriensictis, Cervus, Sus*, a Rhinocerotidae, and *Macaca*. Additional specimens were extracted by us from the calcareous matrix. In this project, the preserved collection was reexamined. Among the 13 species of mammals we identified, three were previously described and figured: a large wild red dog, *Cuon* sp. (Saito, 1939); a Japanese macaque, *Macaca* cf. *fuscata* (Ogino and Otsuka, 2005); and an extinct mustelid, *Oriensictis nipponica* (Ogino and Otsuka, 2008). The materials described in this paper are listed in Table 1. In the National Museum of Japanese History, all of the specimens from the Matsugae Cave are collectively registered as A-636-1-1-35. Hence, we give each specimen the subnumber NMJH-N0101 to NMJH-N0251. All rodent specimens (Reg. nos. NMJH-N0101 to NMJH-N0113, NMJH-N0121 to NMJH-N0127, and NMJH-N0131 to NMJH-N0139), skulls of *Lepus* sp. (NMJH-N0142), *Mustela itatsi* (NMJH-N0161), and *Panthera* sp. (NMJH-N0191), were removed from the calcareous matrix using 3% formic acid. After preparation, the specimens that were previously labeled as "*Felis* sp." (NMJH-N0182) and as "Mustelid sp." (NMJH-N0183) were renamed *Oriensictis nipponica* by Ogino and Otsuka (2008).

The specimens were measured using digital calipers under a microscope. Tooth length was measured as the anteroposterior diameter and width measured along the maximum buccolingual dimension of the crown

Institutional abbreviations.—At present, the specimens of the Matsugae fauna are stored in the National Museum of Japanese History in the Naora Nobuo Collection. The following abbreviations indicate the museums or institutions which store the NAORA Nobuo Collection from Matsugae or the specimens used for comparisons in this study. **IVPP** = Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; **KUPRI-Z** = non-primate vertebrate collection of the Primate Research Institute, Kyoto University, Inuyama, Japan; **KUV** = Department of Veterinary Medicine, Faculty of Agriculture, Kagoshima University, Kagoshima, Japan; **NMJH-N** = NAORA Nobuo Collection, National Museum of Japanese History, Sakura, Japan; **NSM** = National Museum of Nature and Science, Tokyo, Japan; **USNM** = National Museum of Natural History (formerly United States National Museum), Washington D.C., U.S.A.

Dental Abbreviations.—**I (i)**, incisor; **C (c)**, canine; **P (p)**, premolar; **dP (dp)**, deciduous premolar; and **M (m)**, molar; upper- and lower-case letters indicate upper and lower dentitions, respectively.

Other abbreviations.—**QM**, Quaternary Mammal zone of Japanese Islands (Kamei *et al.*, 1988); **L**, tooth length; **W**, tooth width.

Systematic paleontology

Order Rodentia Bowdich, 1821
Family Muridae Gray, 1821
Subfamily Murinae Murray, 1866
Genus ***Apodemus*** Kaup, 1829

Apodemus speciosus (Temminck, 1845a)

Figure 3

Mus speciosus Temminck, 1845a, p. 52.
Apodemus sylvaticus speciosus (Temminck). Naora, 1954, p. 129, fig. 80-1, 2.
Apodemus speciosus (Temminck). Kawamura, 1989, p. 15–57.

Material.—Left M1 (NMJH-N0101, NMJH-N0102, and NMJH-N0105), right M1 (NMJH-N0103 and NMJH-N0104), right M2 (NMJH-N0106), left M2 (NMJH-N0107), right M3 (NMJH-N0108), right m1 (NMJH-N0109 to NMJH-N0111), a left mandible with m1, m2, and m3(NMJH-N0113), and a fragment of right mandible with m1, m2 (NMJH-N0114).

Description.-Dental terminology used in this study is shown in Figure 4. Measurements are listed in Table 2. On M1 (Figure 3A-E), the crown comprises three transverse lophs which show a chevron shape. The anterior chevron is separated from the middle chevron by a deep valley. The middle and posterior chevrons are connected to each other buccally by a narrow ridge formed between the metacone and the hypocone. The metacone is located slightly closer to the middle chevron than the hypocone and posterostyle on the posterior chevron. The posterior cingulum is developed behind the hypocone. The buccolingual width of M2

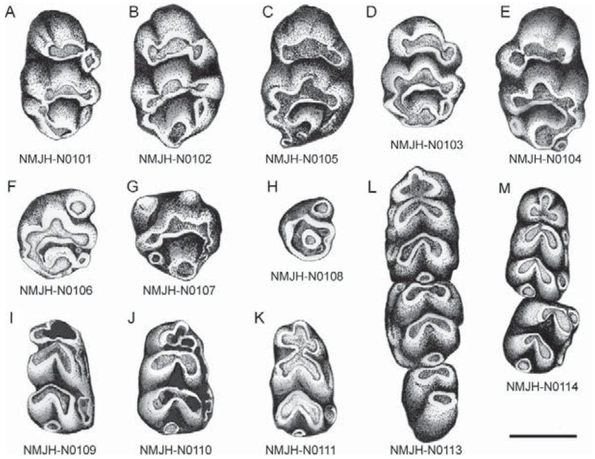


Figure 3. Molars of *Apodemus speciosus* in occlusal view; **A**-**E**, M1; **F** and **G**, M2; **H**, M3; **I**-**K**, m1; **L**, left mandible with m1, m2, m3. Scale bar is 1 mm.

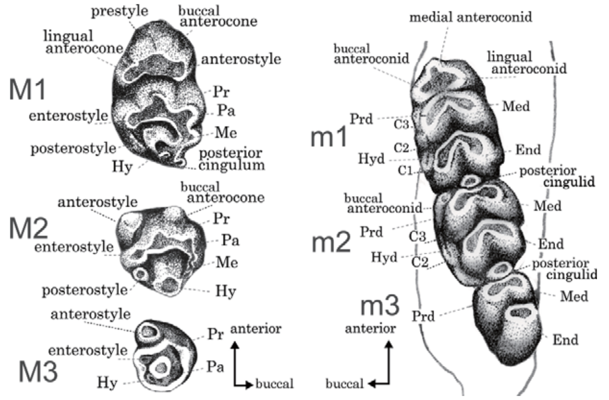


Figure 4. Dental terminology of *Apodemus*.

is broader than the anteroposterior length (Figure 3F). The anterolingually located anterostyle is separated from the anterior chevron by a deep valley. The anterior cingulum (anterocone) is vestigial, but all the Matsugae specimens possess a cingulum. The posterior cingulum is weaker than that of *A. argenteus*. M2 has three roots of which the posterior root is the weakest. M3 (NMJH-N0108; Figure 3H) comprises two laminae and the anterostyle. The anterior and posterior chevrons are connected by buccal and lingual ridges on NMJH-N0108. The anterostyle is separated from the chevron by a deep valley.

The lower first molar possesses three transverse chevrons (Figure 3I–M) In occlusal view, the moderately worn anterior chevron, comprising the buccal, medial, and lingual anteroconids, is trefoil-shaped. The third accessory cusp is placed in the lingual part of the middle chevron. The first and second accessory cusps are located in the lingual part of the posterior chevron. The buccal anteroconid on m2 is separated from the anterior chevron by a deep valley and is located anteriorly to the protoconid (Figure 3L and 3M). In occlusal view, the anteroconid is crescent-shaped. The hypoconid is placed posteriorly to the entoconid. The accessory cusps are located at the lingual margin, and only the second accessory cuspid is developed distinctly. The lower third molar comprises a chevron and a large entoconid (Figure 3L and 3M) The chevron includes the protoconid and metaconid, which are connected to each other anteriorly. The oval entoconid is the largest cuspid.

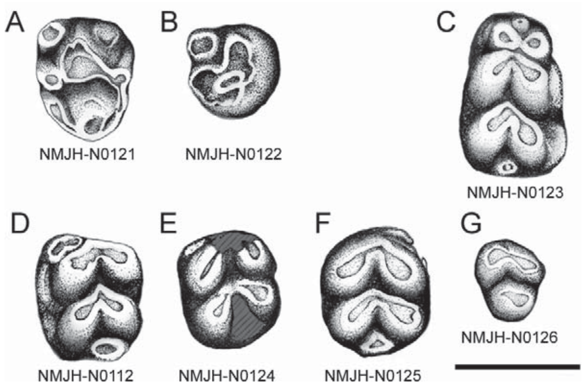


Figure 5. Molars of *Apodemus argenteus* in occlusal view; **A**, M2; **B**, M3; **C**, m1, **D-F**, m2; **G**, m3; **H**, m1 and m2. Scale bar is 1 mm.

Apodemus argenteus (Temminck, 1845b)

Figure 5

Mus argenteus Temminck, 1845b, p. 51.

Material.—Left M2 (NMJH-N0121), left M3 (NMJH-N0122), right m1 (NMJH-N0123), left m2 (NMJH-N0112 and NMJH-N0124), right m2 (NMJH-N0125), right m3 (NMJH-N0126).

Description.—For the dental terminology, see Figure 4. Measurements are listed in Table 2. On M2 (NMJH-N0121; Figure 5A), the positions of the cusps are similar to those in *A. speciosus*; the anteroposterior length is extended further and appears to have a subrectangular shape in occlusal view. The buccal anterocone between the protocone and the paracone is strongly developed. The posterostyle is larger than the metacone. M3 (NMJH-N0122; Figure 5B) is oval in occlusal outline. The anterolingual cusp (anterostyle) is separated from the anterior chevron by a deep valley. The posterior lamina is interrupted by the posterobuccal valley. The lower first molar (m1) is smaller than that of *A. speciosus*. In the early stages of wear of m1 (Figure 5C, H), the med anteroconid is isolated from the anterior chevron. There are two lingual accessory cuspids beside the medial chevron. The accessory cuspids are separated from the medial chevron by a deep valley. The posterior cingulid is small. The lower sec-

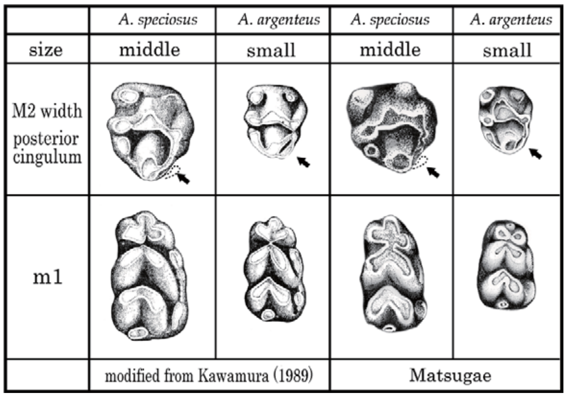


Figure 6. Morphological comparisons of molars between *Apodemus speciosus* and *A. argenteus*.

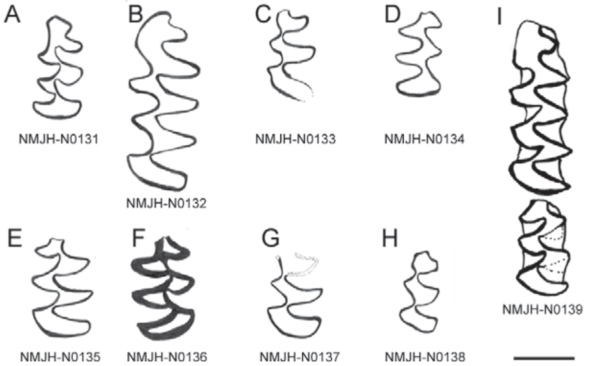


Figure 7. Line drawings of enamel pattern of molars of *Microtus epiratticepoides* in occlusal view; **A**, M3; **B**, m1; **C**-**H**, m2; **I**, left mandible with m1, m2. Scale bar is 1 mm.

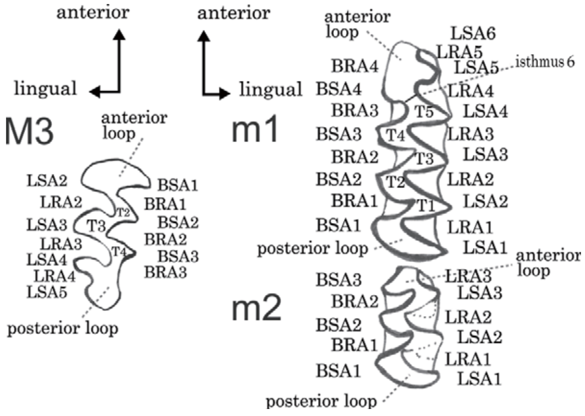


Figure 8. Dental terminology of *Microtus*. **BRA**, buccal reentrant angle; **BSA**, buccal salient angle; **LRA**, lingual reentrant angle; **LSA**, lingual salient angle; **T**, triangle.

ond molar comprises the anterior chevron, posterior chevron, two separate cuspids, and an accessory cuspid in the lingual part of the anterior chevron (Figure 5D–F). The lower third molar is triangular in occlusal outline (Figure 5G). It comprises a chevron and an entoconid. The largest cuspid, the entoconid, is oval in occlusal outline.

Discussion.—Both *Apodemus speciosus* and *A. argenteus* are endemic species distributed in the Japanese main islands except Hokkaido since the middle Pleistocene (Kawamura, 1989). The teeth of *A. argenteus* are smaller than those of *A. speciosus* (Kawamura, 1989). The molars described above are identified with *A. argenteus* on the basis of the following characteristics: the strongly developed posterior cingulum on M2, the absence of the buccal anterocone on M2, and the rectangular shape of m3. However, in M3 (Figure 5B; NMJH-N0122), the posterobuccal valley exists between the protocone and paracone; hence, the posterior lamina is H-shaped in occlusal view. This characteristic is described by Kawamura (1989, p.43, Table 8) as the abnormal type 1 of *A. speciosus*. The enamel pattern of M3 is H-shaped. In *A. argenteus*, M1, M2, and M3 have four, four, and two (or three) roots, respectively, whereas all the upper molars have three roots in *A. speciosus* (Kawamura, 1989). All the upper molars of the Matsugae specimens (NMJH-N0101 to NMJH-N0108) have three roots.

A. speciosus differs from *A. argenteus* in that the former is considerably larger than the latter (Figure 6). The buccolingually relatively narrow M2 and the well developed posterior cingulum on M2 are also characteristics of *A. argenteus.*

Subfamily Arvicolinae Gray, 1821
Genus *Microtus* Schrank, 1798

Microtus epiratticepoides Kawamura, 1988

Figure 7

Microtus montebelli montebelli (Milne-Edwards). Naora, 1954, p. 129, fig. 80-3.

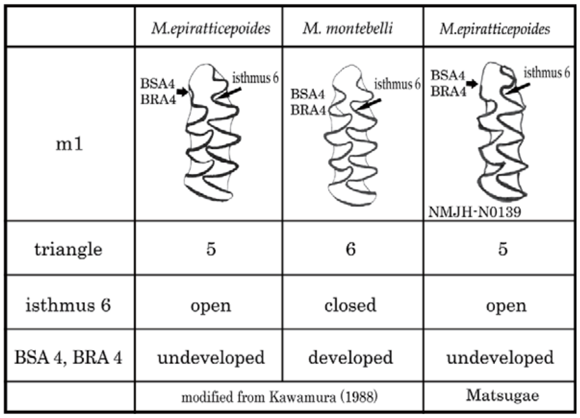
Material.—Left M3 (NMJH-N0131), m1 (NMJH-N0132), and m2 (NMJH-N0133 to NMJH-N0138) and an incomplete left mandible with m1 and m2 (NMJH-N0139).

Description.—The dental terminology is explained in Figure 8. The shape of the isolated left M3 (Figure 7A) is simple, consisting of the anterior loop, three closed triangles (T2, T3, and T4 in Figure 8), and the posterior loop. The buccal salient angles are rather obtuse. The shape of left m1 consists of an anterior loop, four closed triangles and an open triangle, and a posterior loop (Figure 7I). The anterior buccal reentrant angle (BRA) 4 is smaller than the other BRAs (Figure 9). Isthmus 6 is always open to the anterior loop. The isthmus index (=width of isthmus 6/width of isthmus 5; after Kawamura, 1988) is 4.4 on NMJH-N0132 (Figure 7B). The lower second molar comprises four closed triangles and the posterior loop (Figure 7C–I).

Discussion.—The m1 enamel pattern is important in iden-

Table 3. Dental measurements (in mm) of *Lepus* sp.

***Lepus* sp.**	**P2L**	**P2W**	**P3L**	**P3W**	**P4L**	**P4W**
	2.90	4.77	2.83	5.70	3.02	5.41



	M.epiratticepoides	*M. montebelli*	*M.epiratticepoides*
m1	BSA4 BRA4 isthmus 6	BSA4 BRA4 isthmus 6	BSA4 BRA4 isthmus 6 NMJH-N0139
triangle	5	6	5
isthmus 6	open	closed	open
BSA 4, BRA 4	undeveloped	developed	undeveloped
	modified from Kawamura (1988)		Matsugae

Figure 9. Morphological comparison of molars of *Microtus montebelli* and *M. epiratticepoides* (after Kawamura, 1988).

tification of fossil *Microtus* specimens (Kawamura, 1988). In a previous study, Naora (1954) listed *M. montebelli montebelli* in the Matsugae fauna, whereas all the new *Microtus* material discovered from the Matsugae cave deposits are considered not to be *M. montebelli montebelli* but *M. epiratticepoides* on the basis of the following m1 features: five triangles, opened isthmus 6, and reduced BSA4 and BRA4 (Figure 9).

Order Lagomorpha Brandt, 1855
Family Leporidae Gray, 1821
Genus ***Lepus*** Linnaeus, 1758

Lepus sp.

Figure 10

Material.—Left P2, P3, and P4 (NMJH-N0141) and a fragment of skull (NMJH-N0142).

Description.—Measurements are listed in Table 3. The specimen of NMJH-N0142 was labeled as *Lepus brachyurus brachyurus* by Nobuo Naora. The upper second premolar (P2) is large. Three simple anterior reentrant angles (AA) exist on the buccal side. The medial AA possesses weak plicae on the lingual side of the enamel margin. The internal reentrant angle (IA) of P3 possesses plicae of which the anterior row is the mirror image of the posterior. The anterobuccally positioned paracone is reduced. The upper fourth premolar (P4) is similar to P3 in occlusal view but retains a buccally expanded paracone. The IA of P4 also forms two rows of plicae structured symmetrically to one another.

The skull fragment (NMJH-N0142, Figure 10E) was extracted from a block of calcareous sediments of the Matsugae Cave using acetic acid. The skull fragment (NMJH-N0142; Figure 10E) includes part of the left side of the orbit and the zygomatic arch. It is poorly preserved and it is possible that the skull might have been deformed during sedimentation. The posterior supraorbital process is interrupted. The zygomatic process does not protrude sharply.

Discussion.—The leporid dental specimen (NMJH-N0141) is similar to those of *Lepus* because its P2 has three simple AA; however, it differs from *L. brachyurus* in having a large P2 (L 2.9 mm, W 4.8 mm), symmetrical IA on P3 and P4, and a less sharp zygomatic process. On P2, *Pentalagus* and *Oryctolagus* show more complicated AA than NMJH-N0141 (Figure 11). *Pentalagus* also possesses highly complicated plicae on the medial AA of P2 and IA of P3. The upper premolar of *Oryctolagus* is considerably smaller than that of NMJH-N0141. Judging from these characteristics, NMJH-N0141 is closer to *Lepus* than to *Pentalagus* and *Oryctolagus*. *Lepus europaeus* described by Pei (1940) possesses a relatively more complicated AA on P2. *L. wongi* (Teilhard de Chardin and Pei, 1941) and *Lepus* sp. from Choukoutien Loc. 3 have slightly developed medial AA on P2. The P2 characteristics of both Chinese Pleistocene *Lepus* are close to those of NMJH-N0141. However, the buccal margin of P3 is concave, and its IA plicae are simpler than those of NMJH-N0141 (Figure 11).

Generally, species level classification in leporids has been determined and discussed using the morphology of lower first molar (Tomida, 1997). The enamel patterns of the upper premolars indicate that the Matsugae specimens belong to the genus *Lepus*, whereas the characteristics of the premolars are insufficient to assign the specimen to a certain previously known or new species.

Order Carnivora Bowditch, 1821
Family Canidae Gray, 1821
Subfamily Caninae Gill, 1872
Genus ***Cuon*** Hodgson, 1838

Cuon sp.

Cuon sp. Saito, 1939, p. 9–12, 18, pls. 6a, 6b, 9a, 9b.
Cuon sp. Naora, 1958, p. 53–59, figs. 1, 2.

Remarks.—The left maxilla (NMJH-N0151) and the left mandible (NMJH-N0152) are thought to belong to the same individual. The dentitions are considerably worn, which indicates that they belonged to an old individual. In P4, the paracone has crumbled away, and the protocone is completely worn out. The occlusal shape is widened anteroposteriorly. The outline of M1 is triangular in occlusal view; the marginal cingulum is observed at the buccal side between the paracone and metacone; the hypocone is reduced. M2 possesses a deep trigon basin; a marginal cingulum occurs at the buccal side

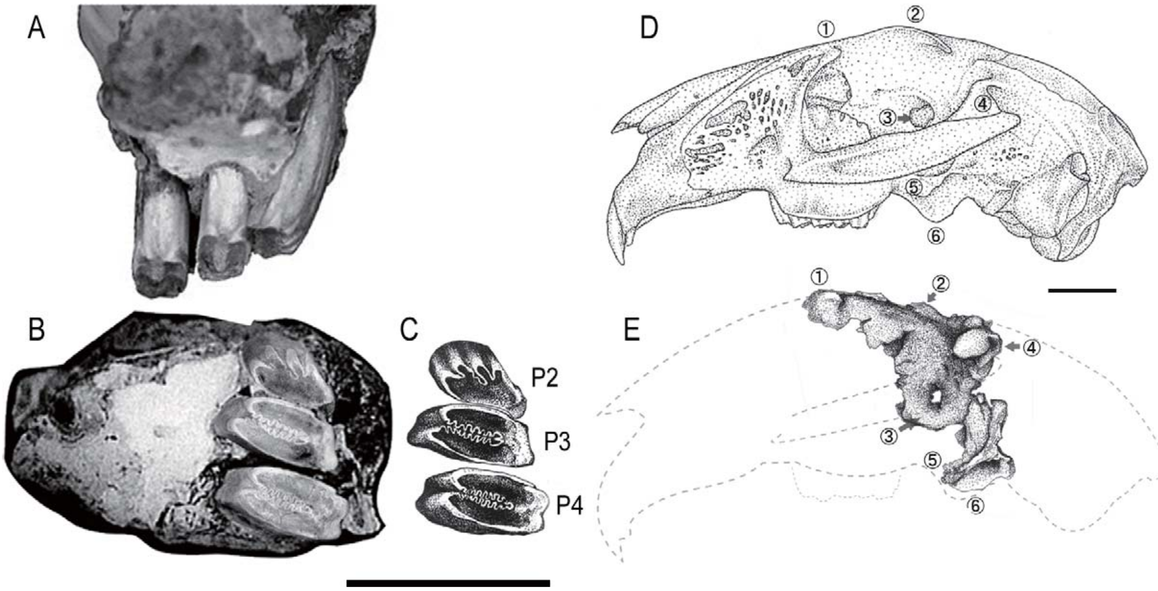


Figure 10. Molars and skull of *Lepus* sp.; **A**, lateral view of skull of *L. brachyurus* (from Abe, 2000); **B**, lateral view of skull (NMJH-N0142); **C**, occlusal view of upper molars (NMJH-N0141). ①, anterior supraorbital process; ②, posterior supraorbital process; ③, optic canal; ④, zygomatic process; ⑤, pterygoid process; ⑥, pterygoid hamulus. Scale bar is 1 cm.

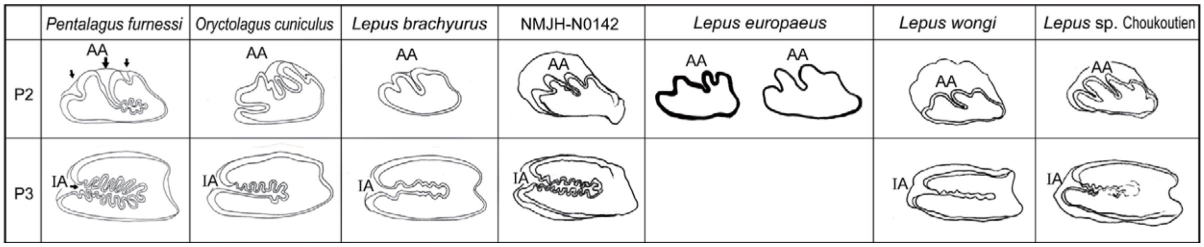


Figure 11. Morphological comparison of molars of East Asian leporids. Figures of *Pentalagus furnessi*, *Oryctolagus cuniculus*, and *Lepus brachyurus* modified from Takamatsu (1997); *L. europaeus* modified from Pei (1940); *L. wongi* modified from Teilhard de Chardin and Pei (1941); *Lepus* sp. from IVPP V02651. Abbreviations: **AA**, anterior reentrant angle; **IA**, internal reentrant angle.

between the paracone and metacone. The crown of m1 is almost crumbled away; however, its length is greater than that of the Japanese wolf, *Canis hodophilax*.

The dimensions of the fossils are equivalent to those of a specimen of *Cuon* cf. *alpinus* (Pei, 1934) Group III from Choukoutien Loc. 1., China (P4, Length 24.2 mm Width 12.5 mm; m1, Length 29.2 mm Width 11.5 mm); however, these sizes differ from Group I and Group II of *Cuon* cf. *alpinus* (Pei, 1934).

The specimens are distinguishable from those of the Japanese wolf, *Canis hodophilax*, in having well developed carnassial teeth (P4 and m1) and somewhat reduced M1. The large tooth size of the specimen and the morphology of the upper cheek teeth indicate that the Matsugae specimen is not *Canis hodophilax* but *Cuon* (Saito, 1939). However, the characteristics of the fragmentary maxilla and mandible from Matsugae are insufficient for establishing a new species.

Subfamily Melinae Burmeister, 1850
Genus ***Meles*** Brisson, 1762

Meles sp.

Figure 12

Meles leucurus kuzuuensis Naora, 1999: appended by Harunari, p. 90–94, fig. 8.

Material.—Right maxilla with broken canine and P2-P4 (NMJH-N0171).

Description.—Measurements are listed in Table 4. The crown of the upper canine is broken. P2 has a single root and a reduced posterior accessory cusp. The anterior root of P3 is directed buccally. Both the anterior and posterior accessory cusps are reduced. P4 has a reduced protocone which is smaller than the hypocone. These characteristics of the premolars indicate that the right maxilla (NMJH-N0171) be-

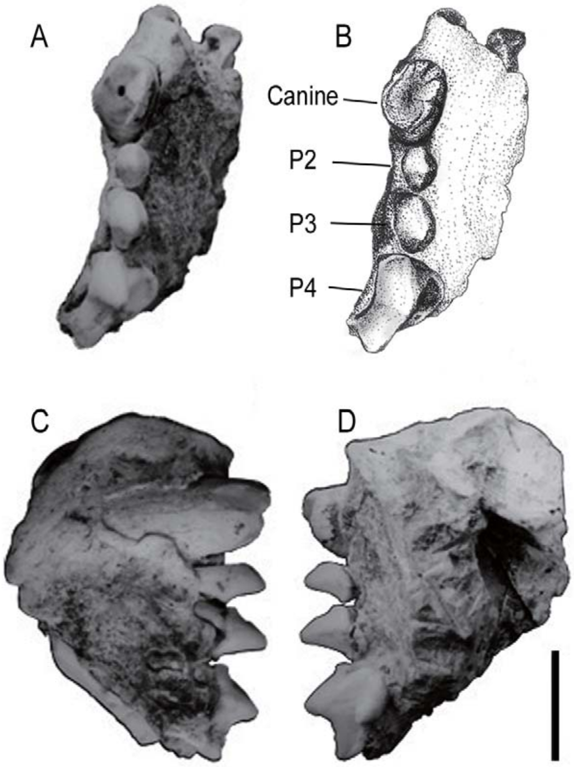


Figure 12. Occlusal view of right maxillary fragment of *Meles* sp. (NMJH-N0171). Scale bar is 1 cm.

longs to *Meles* (Melinae, Mustelidae). The upper canine and P4 are slightly larger than those of an extant Japanese modern population of *Meles meles anakuma* (Table 4).

Discussion.—Three species of extinct Japanese *Meles* (*M. anakuma*, *M. leucurus kuzuuensis*, and *M. mukasianakuma*) are known from the middle Pleistocene Lower Kuzuü fauna (Tochigi Prefecture, eastern Japan) (Shikama, 1949). The upper canine of NMJH-N0171 is slightly larger than that of an extant Japanese population of *M. m. anakuma* and comparable to Eurasian (Old World) badgers, *M. meles* and *M. l. kuzuuensis* (Table 4). P4 of NMJH-N0171 is larger than the other species of *Meles*. Generally, *Meles* tends to show relatively large individual differences in morphology, but the Matsugae specimen is slightly larger than the other Japanese *Meles*.

NMJH-N0171 in the NAORA Nobuo Collection studied here has only one specimen of meline. However, Naora (1954) listed two species of *Meles*. NMJH-N0171 clearly differs from *M. anakuma*, but the characteristics of the premolars of the present specimen are insufficient for a species identification; therefore, the specimen is considered to be *Meles* sp.

Family Mustelidae Fischer, 1817
Subfamily Galictinae Reig, 1957

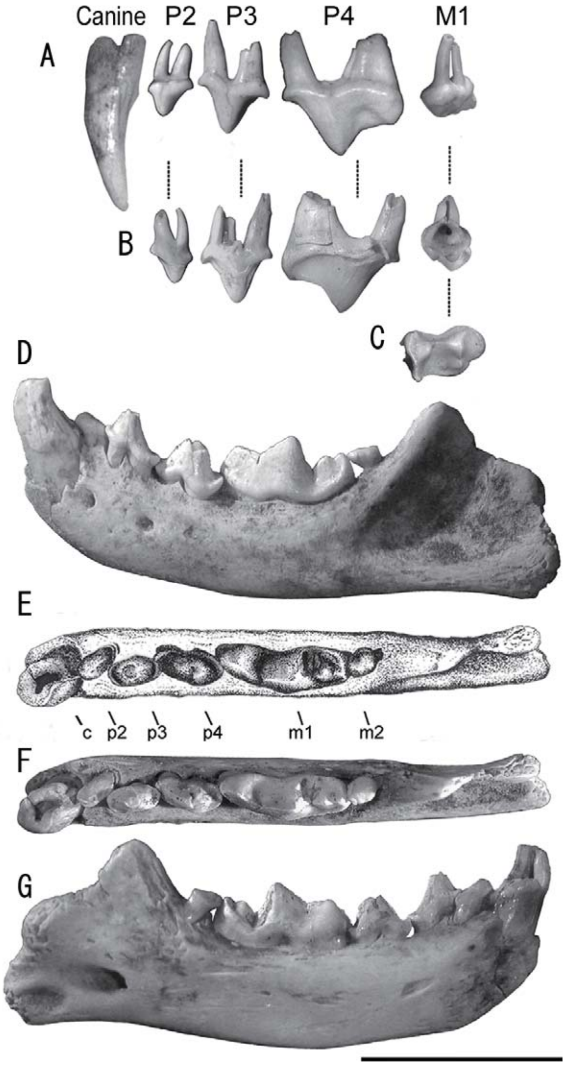


Figure 13. *Mustela itatsi*; **A**, left upper teeth from canine to M1 (NMJH-N0161); **B**, left mandible with i2, i3, c-m2 (NMJH-N0162). Scale bar is 1 cm.

Tribe Galictini Baskin, 1998
Genus ***Oriensictis*** Ogino and Otsuka, 2008

Oriensictis nipponica (Naora, 1968)

Lutra nipponica Naora, 1968, p. 1–11, figs. 1–3.
Oriensictis nipponica (Naora). Ogino and Otsuka, 2008, p. 159–166, fig. 1.

Remarks.—The three specimens comprising two maxillae and a mandible with teeth (NMJH-N0181–0183) were described by Ogino and Otsuka (2008). They determined that these specimens and *Lutra nipponica* in Naora (1968) belonged to the same species, and subsequently established a new genus, *Oriensictis* (Galictini, Mustelidae). *Lutra melina* from the middle Pleistocene Locality 1 of Choukoutien fauna (northern China) also belongs to the genus *Oriensictis* (Ogino

Table 4. Dental measurements (in mm) of *Meles*.

	CL	**CW**	**P2L**	**P2W**	**P3L**	**P3W**	**P4L**	**P4W**	**M1L**	**M1W**	**Remarks**
***Meles* sp.**	7.07	5.42	4.25	3.03	5.45	3.58	9.01	7.29	—	—	NMJH-N0171
M. anakuma	6.00	4.20	3.30	2.70	5.50	3.30	8.00	6.00	11.07	9.83	Shikama, 1949
M. leucurus kuzuuensis	6.00	5.00	4.00	3.00	5.70	4.30	8.80	7.50	11.30	10.80	Shikama, 1949 (Holotype)
M. mukasianakuma	—	—	—	—	6.50	4.40	—	—	9.80	11.10	Shikama, 1949
M. meles	7.29	5.27	4.40	3.09	5.71	3.93	8.24	7.04	12.98	11.48	USNM257676
M. meles anakuma	6.00	4.20	3.30	2.70	5.50	3.30	8.00	6.50	11.50	10.00	Shikama, 1949

Table 5. Dental measurements (in mm) of *Mustela itatsi*.

Mustela itatsi	**CL**	**CW**	**P2L**	**P2W**	**P3L**	**P3W**	**P4L**	**P4W**	**M1L**	**M1W**		
	3.49	—	2.31	1.08	3.47	1.82	6.00	—	3.53	—		
	cL	**cW**	**p2L**	**p2W**	**p3L**	**p3W**	**p4L**	**p4W**	**m1L**	**m1W**	**m2L**	**m2W**
	3.10	2.57	1.50	1.29	2.91	1.34	3.40	2.00	6.91	2.28	1.55	1.40

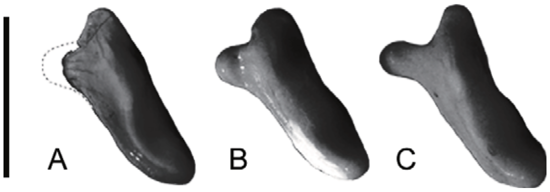


Figure 14. Morphological comparison of P4 of East Asian *Mustela*. **A**, *M. itatsi* (NMJH-N0161); **B**, *M. itatsi* (KUV81); **C**, *M. sibirica* (KUV31). Scale bar is 5 mm.

and Otsuka, 2008). *Oriensictis* is the only grison discovered in the middle Pleistocene of East Asia.

Genus ***Mustela*** Linnaeus, 1758

Mustela itatsi Temminck, 1844

Figure 13

Material.—Left upper tooth row (C-M1) (NMJH-N0161) and left mandible with i2, i3, c-m2 (NMJH-N0162).

Description.—Measurements are listed in Table 5. NMJH-N0161 and NMJH-N0162 belong to the same individual. The upper canine is moderately large. Neither P1or p1 are present. P2 and P3 are double-rooted, and these teeth have one main cusp and anterior and posterior accessory cusps. P4 has three cusps, which form a y-shaped outline of the crown in occlusal view. The buccal notch between the paracone and protocone is weak, as in *M. itatsi* (Abe, 2000). The largest cusp, the paracone, possesses a small buccal parastyle. M1 expands buccolingually, and deep notches exist between the paracone and protocone. The paracone possesses an anterobuccal cingulum. The lower canine is slightly curved posteriorly. The lower second premolar (p2) possesses two roots. Both p3 and p4 are unicuspid accompanied by anterior and posterior cingulids. The metaconid has crumbled away. The lingual side of the talonid basin of m1 is open. The entoconid is located posterobuccally. The lower second molar (m2) is reduced.

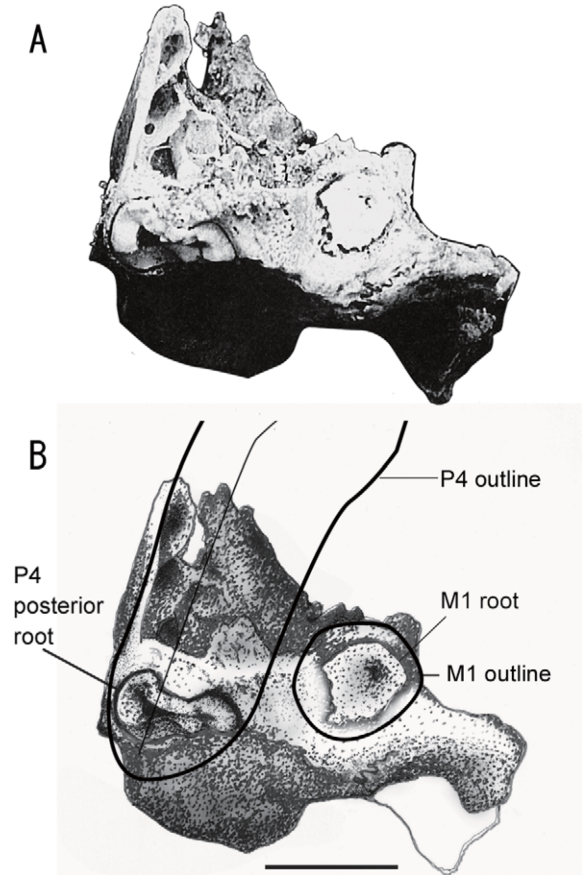


Figure 15. *Panthera* sp. (NMJH-N0191). Right maxilla with posterior root of P4 and root of M1. Scale bar is 1 cm.

Discussion.—The size of the present specimens is comparable to a male individual of the Japanese weasel, *Mustela*

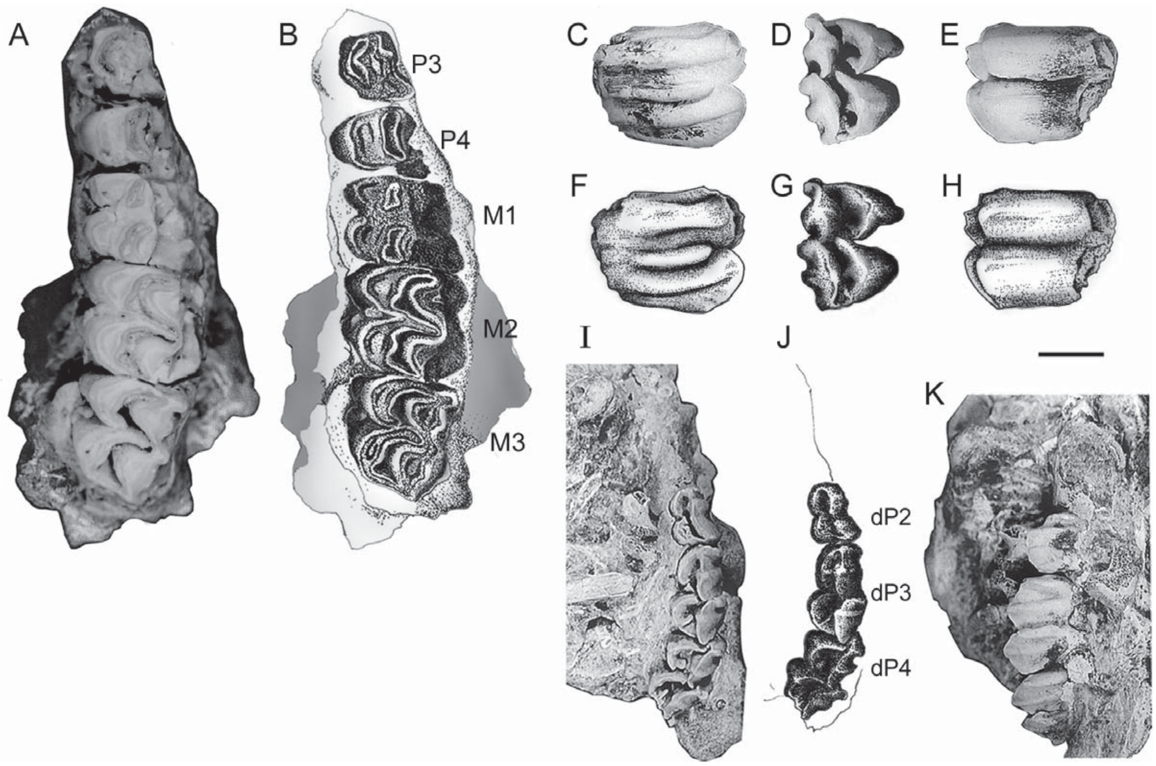


Figure 16. Upper cheek tooth of *Cervus* sp., **A**, occlusal view of left tooth row (NMJH-N0211); **B**, occlusal view of left deciduous tooth (NMJH-N0213); buccal (**C**), occlusal (**D**), and lingual (**E**) views of right M3 (NMJH-N0212). Scale bar is 1 cm.

itatsi and a male individual of the Siberian weasel, *M. sibirica*. On P4, *M. itatsi* possesses a relatively less developed protocone and a shallower buccal notch between the protocone and the paracone than in *M. sibirica* (Figure 14). Judging from the characteristics of P4, the Matsugae specimens are identified as *M. itatsi*.

Family Felidae Gray, 1821
Subfamily Pantherinae Pocock, 1917
Genus ***Panthera*** Oken, 1816

Panthera sp.

Figure 15

Material.—Right maxilla with the posterior root of P4 and the root of M1 (NMJH-N0191).

Description and discussion.—The M1 alveolus is located rather anteriorly relative to the posterior root of P4. This maxilla is apparently larger than that of *Felis* and *Lynx*; therefore, the specimen is considered to be *Panthera* sp.

Order Cetartiodactyla Montgelard, Catzeflis, and Douzery, 1997
Family Cervidae Gray, 1821
Subfamily Cervinae Baird, 1857
Genus ***Cervus*** Linnaeus, 1758

Cervus sp.

Figure 16

Material.—Left upper tooth row P3-M3 (NMJH-N0211), isolated right M3 (NMJH-N0212), dP2-dP4 (NMJH-N0213).

Description.—Measurements are listed in Table 6. A right upper tooth row (NMJH-N0211) preserves P3-M3, all of which are heavily worn. The buccal enamel walls of P3-M2 are damaged. The upper third molar (M3) has well developed buccal parastyle, mesostyle, and metastyle. M2 and M3 have a lingual accessory column between the protocone and hypocone. M3 (NMJH-N0212) is rectangular in occlusal outline with nearly straight posterior margin; the protocone has anterior and posterior wings on the lingual wall of the lobe; the metaconule also has a well developed posterior wing. The metaconule of dP2-dP4 has a posterior wing on each lingual wall. The wing on dP2 is more complicated. The protocone of dP4 also has a posterior wing on the lingual wall.

Discussion.—Five species of fossil *Cervus* (*C. elaphus*, *C. grayi katokiyomasai*, *C. nippon*, and *C. praenipponicus*) are known from the Pleistocene of the Japanese Islands, and *C. nippon* has four subspecies (*C. n. nippon*, *C. n. centralis*, *C. n. mageshimae*, and *C. n. yakushimae*) (Shikama, 1949; Kuwayama *et al.*, 1998). These Japanese *Cervus* have been described based on the morphological characteristics

Table 6. Dental measurements (in mm) of *Cervus* sp. Asterisks mean broken tooth.

***Cervus* sp.**	**P3L**	**P3W**	**P4L**	**P4W**	**M1L**	**M1W**	**M2L**	**M2W**	**M3L**	**M3W**
	12.83	16.20*	13.80*	16.42	14.30*	19.20*	17.88	20.20*	20.18	18.2
***Cervus* sp.**	**dP2L**	**dP2W**	**dP3L**	**dP3W**	**dP4L**	**dP4W**				
(juvenile)	12.57	9.18	18.83	11.22	19.43	16.75				

of skull, pedicles, and antlers. The measurements of tooth rows among the species cannot distinguish one species from another. Therefore, it is difficult to decide the precise taxonomic position of the Matsugae specimens on the basis of the dental morphology alone. Nevertheless, two M3 of the Matsugae specimens (NMJH-N0211 and NMJH-N0212) possess a more robust metastyle on P2 than that of the modern Japanese deer, *C. nippon* including its four subspecies. A stout metastyle in P2 and well developed buccal styles in M3 are also observed in *C. grayi.* The dental characteristics and size of the Matsugae specimens are close to those of *C. grayi* but the M3 is narrower.

The length and width of NMJH-N0211 are 20.2 mm and 18.2 mm, respectively. The length and width of NMJH-N0212 are 20.6 mm and 17.4 mm, respectively. As shown in Figure 19, two upper third molars (NMJH-N0211 and NMJH-N0212) are much larger than modern *C. nippon*. The range of the M3 length of Chinese *C. grayi* is 20.0 to 22.1 mm (N=8, mean 20.9 mm) and the width is 19.7 to 21.7 mm (mean 20.8 mm). The range of the M3 length of *C. nippon* is 15.0 to 18.9 mm (N=10, mean 17.1 mm) and the width is 14.3 to 18.0 mm (mean 16.8 mm). The lengths of M3 of the Matsugae specimens are rather close to those of the Chinese *C. grayi* although the width is narrower.

C. elaphus and *C. grayi katokiyomasai* are defined using the morphology of the antler; therefore, it is impossible to compare the Matsugae specimens with them.

Family Suidae Gray, 1821
Subfamily Suinae Gray, 1821
Genus ***Sus*** Linnaeus, 1758

Sus scrofa Linnaeus, 1758

Figure 17

Material.—Right maxilla with P1-P4 (NMJH-N0251).

Description.—Measurements are listed in Table 7. The fragment of a right maxilla (NMJH-N0251) retains alveoli of the canine and worn premolars. The posterior part of P4 is broken. P1 has two roots. The crown is completely worn out and it is impossible to observe its morphological characteristics. The crown of P2 is also worn out although the posterior part shows faint enamel plicae. The posterolingually located protocone is separated from the metacone by a deep valley. A widely developed posterior cingulum is attached to the buccal part of P3. The anteroposterior length of P3 is longer than the buccolingual width. The posterolingually located protocone is wide and has a small anterior cusp. The anterolingually located primocone has indented enamel. The anterior and posterior cingula are well developed. P4 is more molarized than P3. The incomplete P4 retains the paracone, protocone,

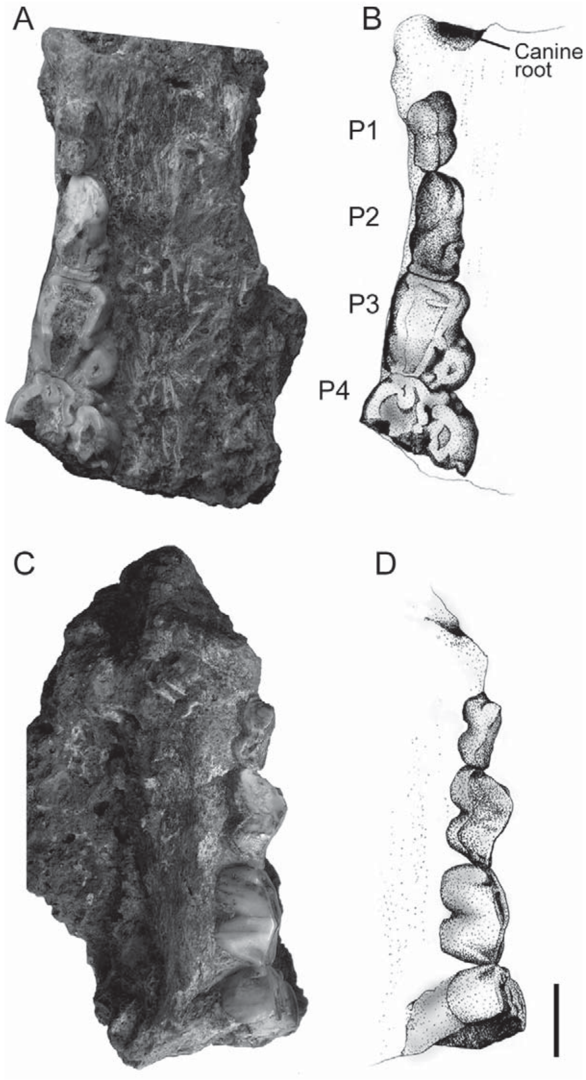


Figure 17. Right maxillary fragment of *Sus scrofa* (NMJH-N0251). **A**, occlusal view; **B**, lingual view of upper teeth from P1 to P4. Scale bar is 1 cm.

Table 7. Dental measurements (in mm) of *Sus*. Asterisks mean broken tooth.

	P1L	P2W	P2L	P2W	P3L	P3W	P4L	P4W	Production area	Remarks
Sus scrofa	9.66	4.11*	14.25	7.26	14.27	12.4	—	16.33*	Matsugae	
S. cf. *lydekkeri*	9.30	4.60	11.50	—	14.30	11.30	13.90	14.90	Kanagawa	Shikama and Hasegawa, 1965
Sus lydekkeri	—	—	13.00-15.00	9.50	12.00-16.00	9.00-14.00	13.00-17.00	15.00-17.00	Choukoutien	Young, 1932
Sus lydekkeri	—	—	14.20	9.50	15.40	13.80	—	—	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	15.20	—	—	—	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	14.60	13.40	—	—	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	12.90	12.40	—	—	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	—	—	16.50	17.00	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	—	—	14.70	15.20	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	—	—	14.20	16.40	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	—	—	14.00	16.00	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	—	—	13.90	16.30	Choukoutien	Zdansky, 1928
Sus lydekkeri	—	—	—	—	—	—	13.20	16.30	Choukoutien	Zdansky, 1928
Sus scrofa	—	—	—	—	13.60	10.50	12.90	14.70	Akiyoshi	Shikama and Okafuji 1958
Sus scrofa	—	—	—	—	12.00	9.00	12.50	12.50	Kokura	Shikama, 1936
Sus scrofa	8.7	3.83	12.26	7.34	13.02	9.91	11.62	13.65		# 929: KUPRI-Z.Z
Sus scrofa	9.07	4.28	12.81	7.63	13.93	10.63	12.32	14.22		#1121: KUPRI-Z.Z
Sus scrofa	7.61	3.63	10.9	6.21	12.79	9.04	10.96	12.87		#1123: KUPRI-Z.Z
Sus scrofa	7.72	3.92	11.17	6.84	12.93	9.8	12.22	14.53		#1132: KUPRI-Z.Z
Sus scrofa	7.04	3.51	11.62	7.33	13.24	10.09	11.18	13.85		#1135: KUPRI-Z.Z
Sus scrofa	7.37	3.88	10.22	6.06	11.59	8.71	10.45	12.59		#1137: KUPRI-Z.Z
Sus scrofa	9.02	4.08	10.64	6.71	13.01	10.58	12.1	13.36		#1129: KUPRI-Z.Z
Sus scrofa	8.21	3.42	12.38	7.61	12.48	10.66	11.87	13.61		#1136: KUPRI-Z.Z
Sus scrofa	8.99	3.99	11.08	6.75	11.42	9.21	10.61	11.87		#1124: KUPRI-Z.Z
Sus scrofa	8.39	3.98	10.92	6.55	13.16	9.59	11.74	13.01		#1138: KUPRI-Z.Z
Sus scrofa	7.44	3.85	11.27	6.21	11.84	8.87	10.08	12.68		#1041: KUPRI-Z.Z

Table 8. Dental measurements (in mm) of *Dicerorhinus* sp.

***Dicerorhinus* sp.**	**dP4L**	**dP4W**	**dpL**	**dpW**
	49.40	47.29	50.41	27.00

protofossa, and anterior cingulum. The buccolingual width at the anterior part is much wider than that of the modern *Sus scrofa*. The paracone is two times bigger than the protocone. The buccal cingulum that seems to be constructed by the conjoined anterior conules is widely developed and surrounds P3. Two small conules are also positioned along the anterolingual part of the protocone. The valley between the anterior conules and the protocone is narrow and the protocone is oriented anteriorly. The protocone is separated from the paracone by a distinct protofossa.

Discussion.—The genus *Sus* from the middle Pleistocene Japanese mainland is represented by *S. scrofa*, *S. nipponicus*, and *S. lydekkeri* (Shikama, 1949, Shikama and Okafuji, 1965). Naora (1954) listed *Sus nipponicus* in the faunal list of the Matsugae Cave. In contrast, Fujita *et al*. (2001) reexamined Japanese Quaternary wild boars and concluded that the middle Pleistocene Japanese *Sus* show a marked tendency to be larger than the modern Japanese *S. scrofa*. The middle

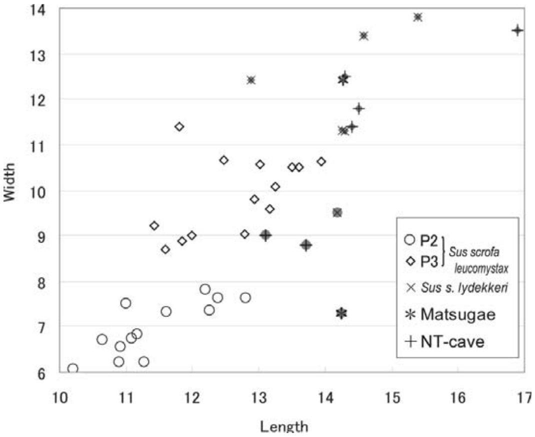


Figure 18. Comparison of P2 and P3 length and width of Chinese '*Sus lydekkeri*' and Japanese *S. scrofa*. Open symbols mean modern specimen and closed symbols mean fossil ones. The measurements are listed in Table 8.

Pleistocene Japanese *Sus* has been included in these variations of *S. scrofa*. Fujita (2001) also concluded that "*S. lydekkeri*" is indistinguishable from the middle Pleistocene *S. scrofa*, and suggested that "*S. lydekkeri*" should be treated

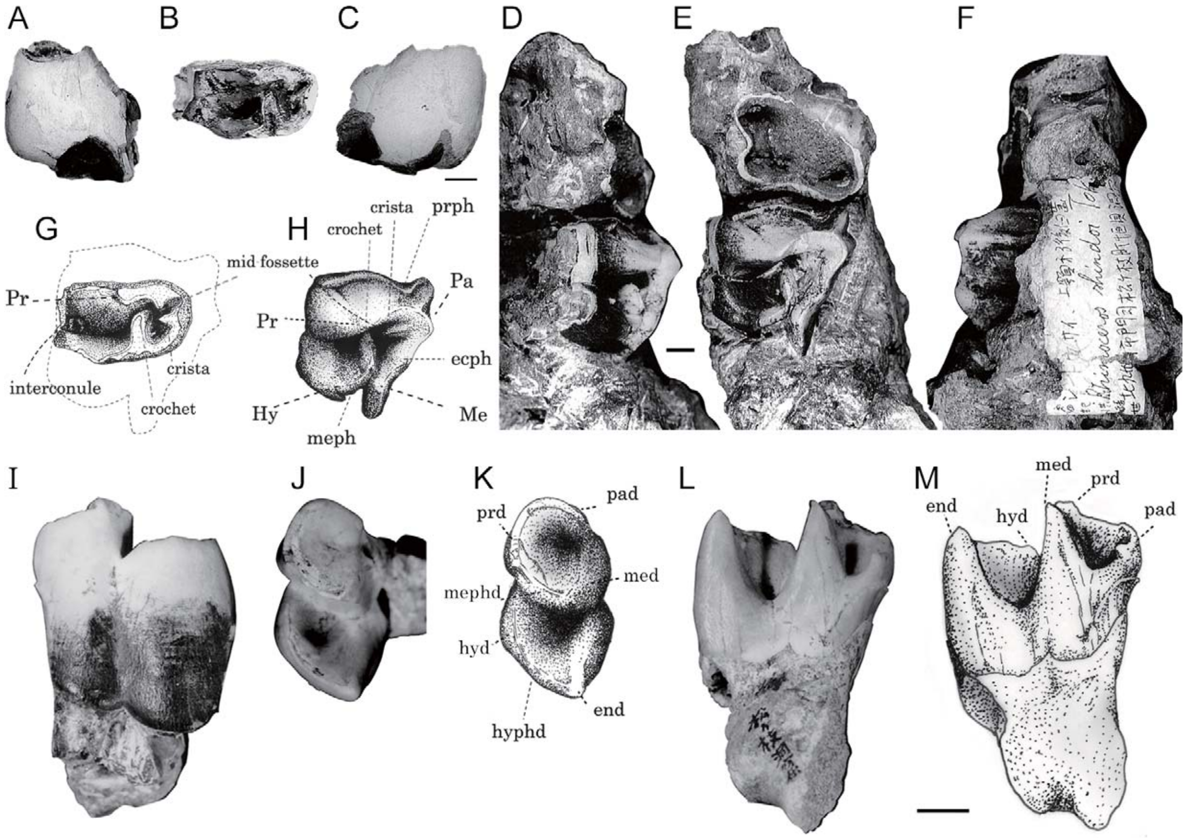


Figure 19. Molars of *Dicerorhinus* sp.; Left M2 (NMJH-N0203), occlusal (**A**) and lingual (**B**); dP4 (NMJH-N0201), occlusal(**C**) and lingual (**D**); lower deciduous tooth (NMJH-N0202), occlusal(**E**) and lingual (**F**). Scale bar is 1 cm.

as a chronological subspecies of *S. scrofa*, namely *S. s. lydekkeri*. The tooth size of NMJH-N0251 is obviously larger than that of the modern Japanese *S. scrofa* and comparable to the middle Pleistocene Chinese "*S. lydekkeri*" and middle Pleistocene *S. scrofa* from NT Cave in Okayama Prefecture (Figure 18). P2 of NMJH-N0251 is anteroposteriorly longer than that of modern *S. scrofa*. The width measurements of P3 and P4 are also obviously larger. The wide P3 is due to the well developed protocone.

Shikama and Hasegawa (1965) described *Sus* cf. *lydekkeri* from the late Pliocene Zushi mudstone member of the Miura Group, Kanagawa Prefecture, eastern Japan. This specimen bears a small dentition comparable to that of *S. scrofa*. P3 size and transverse width of P4 of *Sus* cf. *lydekkeri* from Kanagawa are not as great as those of Chinese "*S. lydekkeri*" (Zdansky, 1928; Young, 1932) and NMJH-N0251.

NMJH-N0251 retains only right upper premolars. These premolars are heavily worn and the morphological characteristics are unclear. Moreover, *Sus* is usually diagnosed by the morphology of skull and molars; therefore, it is difficult to assign NMJH-N0251 to a subspecies, but it might be included in the large-sized type of *S. scrofa* such as *S. s. lydekkeri*.

"*S. lydekkeri*" is one of the representatives of the middle Pleistocene Choukoutien fauna. The similarity of "*S. lydekkeri*" to NMJH-N0251 indicates that the Matsugae fauna is close in geological age to the Choukoutien fauna and that faunal exchange existed between them.

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Owen, 1845
Genus ***Dicerorhinus*** Gloger, 1841

Dicerorhinus sp.

Figure 19

Material.—Left dP4 (NMJH-N0201), left lower deciduous cheek tooth (NMJH-N0202), left M2 (NMJH-N0203).

Description.—For the dental terminology, see Figure 19G, H, and K. Measurements are listed in Table 8. The fragment of M2 (NMJH-N0203) preserves only a part of the mid-fosette. The mid-fossette is more complicated in M2 than in dP4 (NMJH-N0201). The crista is located on the buccal side, the anticrochet is developed on the medial side of the protoloph, and several plicae are present in the fossette.

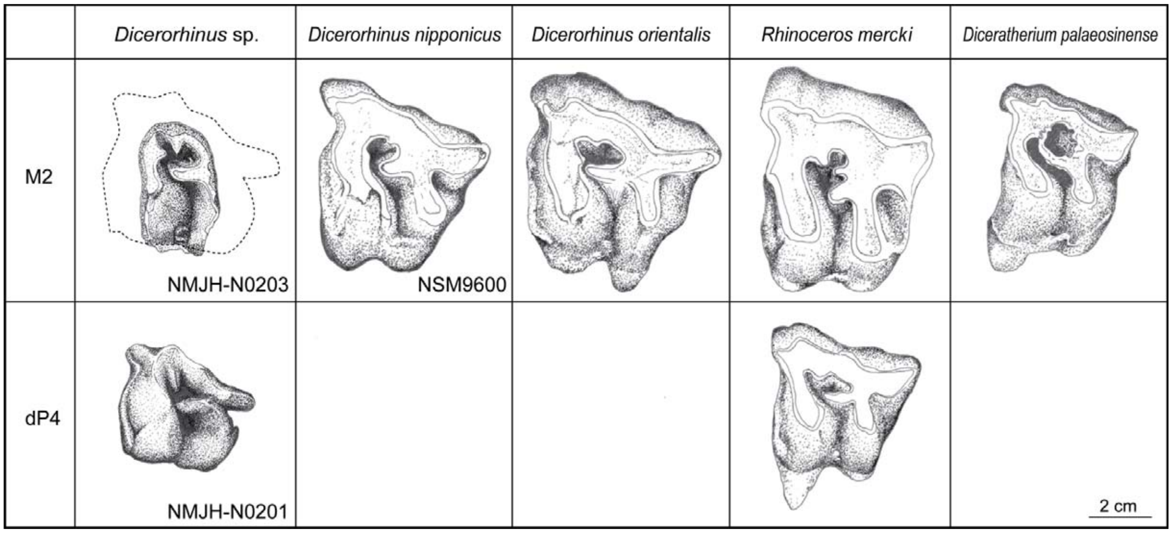


Figure 20. Morphological comparison of the mandible of East Asian rhinocerotids. Figure of *Rhinoceros merchi* was modified from Teilhard de Chardin (1941); *Dicerorhinus orientalis* and *Diceratherium palaeosinense* are modified from Ringström (1924).

These characteristics are close to those of the Mio-Pliocene Chinese *Dicerorhinus orientalis* (Ringström, 1924) and the middle Pleistocene Japanese *D. nipponicus* (Shikama *et al.*, 1967). NMJH-N0203 has an interconule on the lingual side of the protocone-hypocone ridge. The dP4 (NMJH-N0201) is unworn and well preserved. It is trapezoidal in outline in occlusal view, and has four cusps and three lophs (ectoloph, protoloph, and metaloph). The highest cusp is the paracone, which has two slopes on the anterolingual surface. The height of the metaloph is slightly lower than that of the other lophs and the notch between the hypocone and metacone is shallow. A large crista is located in the buccal side of the mid-fossette. There are accessory cusps on the anterobuccal edge of the paracone and the posterior edge of the hypocone. The dP4 (NMJH-N0201) also possesses an interconule on the lingual side of the protocone-hypocone ridge. The lower deciduous tooth, NMJH-N0202, comprises a pair of U-shaped lophid, the metalophid between the protoconid and metaconid and the hypolophid between the hypoconid and entoconid. A distinct anterior flange is present on the medial surface and a weak posterior flange is present on the distal surface.

Discussion.—The crown of M2 (NMJH-N0203) is broken; therefore, it is impossible to determine its size. However, it is distinctly smaller than that of the Chinese rhinocerotid; *Rhinoceros mercki* (=*Stephanorhinus kirchbergensis*: synonymized by Billia, 2008) and *Diceratherium palaeosinensis* (Ringström, 1924) (Figure 20). Based on the position of the crista and anticrochet of M2, the Matsugae specimen is close to *Dicerorhinus orientalis* (=*Stephanorhinus kirchbergensis* synonymized by Billia, 2008) and *Dicerorhinus nipponicus* (Shikama *et al.*, 1967). Furthermore, the enamel patterns of M2 indicate that the present specimens belong to the genus *Dicerorhinus*. Based on these characteristics, we conclude that the Matsugae specimens are assigned to *Dicerorhinus*; however, the preservation of this molar from Matsugae is insufficient to determine its taxonomic assignment at the species level.

Okazaki (2006) reported other Matsugae rhinocerotid material, including a mandible with deciduous teeth and two isolated upper deciduous teeth stored in the anatomical laboratory of the Faculty of Medicine, Kyushu University, and two isolated upper deciduous teeth stored in the Kyushu Institute of Technology. He stated that these Matsugae specimens are comparable to the undescribed specimen from the middle Pleistocene Lower Kuzuü fauna, Tochigi Prefecture, eastern Japan. These rhinocerotid specimens should also be considered to represent the same genus.

The rhinocerotid fossils from the Matsugae cave deposits were named "*Rhinoceros shindoi*" by Tokunaga (1931) without any description; they have remained undescribed until now. Some of the *Rhinoceros* material in Asia has been synonymized into other rhinocerotid genera after systematic revision (e.g., Billia, 2008), and we identify the Matsugae rhinocerotid as *Dicerorhinus* rather than *Rhinoceros*. Thus, we doubt the presence of *Rhinoceros* in the Matsugae Cave, and consider "*Rhinoceros shindoi*" to be invalid.

Billia (2008) pointed out that the Pleistocene "tandem-horned" Eurasian interglacial rhinoceros such as "*Rhinoceros mercki*" and "*Dicerorhinus mercki*" should be regarded as synonyms of *Stephanorhinus kirchbergensis* Jäger (1839). In Japan, the middle Pleistocene *Dicerorhinus nipponicus* and *Dicerorhinus* sp. from the Matsugae cave deposit are also comparable to the Eurasian *S. kirchbergensis*. In future stud-

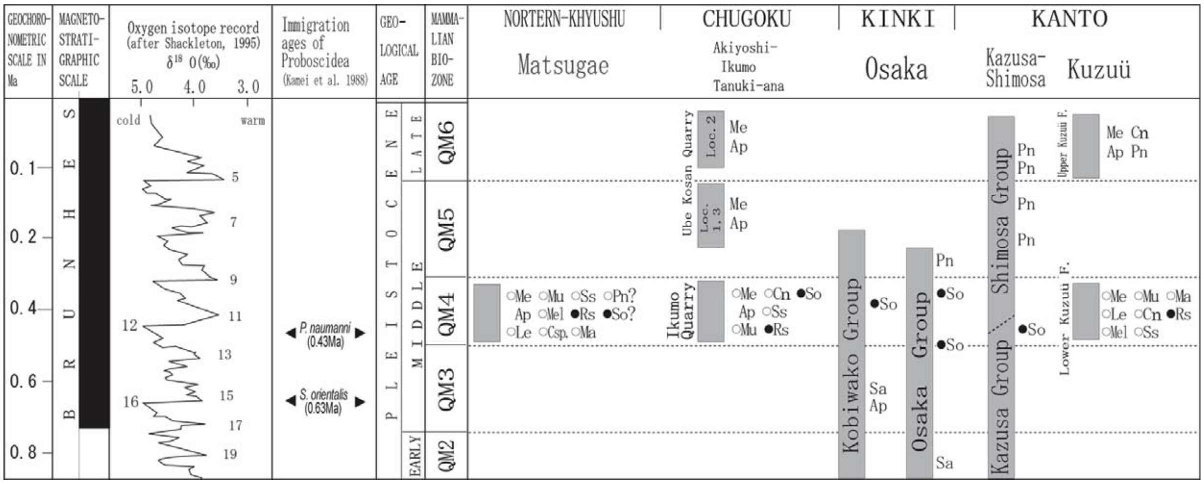


Figure 21. Correlation of middle and late Quaternary mammalian fauna in Japan. **Ap**, *Apodemus speciosus*; **Cn**, *Cervus nippon*; **Csp.**, *Cervus* sp.; **Le**, *Lepus*; **Ma**, *Macaca*; **Me**, *Microtus epiratticepoides*; **Mel**, *Meles*; **Mu**, *Mustela itatsi*; **Pn**, *Palaeoloxodon naumanni*; **Rs**, rhinocerotids; **Sa**, *Stegodon aurorae*; **So**, *Stegodon orientalis*; **Ss**, *Sus scrofa*. Open circles mean lower limit of the taxa. Closed circles mean upper limit of the taxa (after Kamei *et al*., 1988).

ies on the middle Pleistocene Japanese *Dicerorhinus*, the possibilities of ascribing them to *Stephanorhinus* should be kept in mind.

Order Primates Linnaeus, 1758
Family Cercopithecidae Gray, 1821
Subfamily Cercopithecinae Blanford, 1888
Genus ***Macaca*** Lacépède, 1799

Macaca sp. cf. ***M. fuscata*** Blyth, 1875

Macaca sp. cf. *M. fuscata* Blyth, 1875. Ogino and Otsuka, 2005, p. 1–9. figs. 1, 4.

Remarks.—A skull with dP3–4 (NMJH-N0241) was described as *Macaca* sp. cf. *M. fuscata* by Ogino and Otsuka (2005, in Japanese). The bony tissue has almost exfoliated but the skull was filled by calcareous matrix that retains the cast of the brain case. The nasal and premaxilla bones are lost. The base of the left zygomatic arch, which has a thin outline, is present. Left dP3 and dP4 are bilophodont with four cusps. The buccal cusps are slightly higher than the lingual cusps. The buccolingual width of the paracone-metacone ridge is greater than that of the metacone-hypocone ridge. A small interconule is present at the lingual side of dP4 and a rudimentary pit occurs on the anterolingual surface.

Ogino and Otsuka (2005) compared the Matsugae *Macaca* cf. *fuscata* with the modern East Asian “*fascicularis*” group (Fooden, 1976), the middle Pleistocene northern Chinese *M. andersoni* (Schlosser, 1924) and *M. robusta* (Young, 1934), and the late Pleistocene Japanese *M. fuscata* (Shikama, 1949) from the Upper Kuzuü Formation. The results of their study indicated that the deciduous teeth of Pleistocene Japanese *M. fuscata* are larger than those of the modern *fascicularis* group. However, statistic analyses (the Mahalanobis test) revealed that the Matsugae skull (NMJH-N0241) is not outside the Mahalanobis ellipses of modern *M. fuscata*, meaning that the Matsugae skull does not differ significantly from modern *M. fuscata* (significance level=5%; Ogino and Otsuka, 2005). According to Shigehara *et al*. (2002), Pleistocene *M. fuscata* generally shows a tendency to enlargement in molar size. Although the time gap exceeds 0.35 Ma between the Matsugae fauna (around 0.43 Ma) and Upper Kuzuü fauna (younger than 0.07 Ma), the results support the inference that the size of the ancestors of the Japanese macaque increased throughout the Pleistocene. Ogino and Otsuka (2005) suggested that the ancestor of the Japanese macaque likely has a close relationship with the large Chinese fossil macaques, *M. andersoni* and *M. robusta*.

General discussion and conclusion

Kawamura (1991, 1998) and Konishi and Yoshikawa (1999) discussed timing of the immigrations of terrestrial mammals from the Asian continent to the Japanese Islands during the Pleistocene. It has been suggested that middle Pleistocene land connections were established at 0.63 Ma (Oriental elements; southern Chinese *Stegodon* stage) and 0.43 Ma (Palearctic elements; northern Chinese *Palaeoloxodon* stage). The proboscideans are indices of the Quaternary Mammal zones of Japanese Islands (Kamei *et al.*, 1988). *S. orientalis* is an index fossil of QM4, which is correlated to the middle level of the middle Pleistocene, and is considered to belong to the immigrants of the middle Pleistocene first land connection (0.63 Ma), whereas *P. naumanni* is an index

Table 9. List of the middle Pleistocene Japanese mammal Fauna. Open circles are lost materials. [1]Otsuka (1989); [2]Hasegawa (1980); [3]Shikama (1949).

	Bisan-Seto[1]	Matsugae	Ikumo[2]	Kuzuü[3]
Apodemus		●	●	
Microtus		●	●	●
Lepus		●		●
Canis		○		●
Cuon		●		●
Meles		●		●
Mustela		●	●	●
Oriensictis		●		
Panthera	●	●		●
Cervus	●	●	●	●
Sus scrofa		●	●	●
Rhinocerotid		●	●	●
Macaca		●		●
Palaeoloxodon	●	○		●
Stegodon	●	○	●	

fossil of QM5, which is correlated to the upper level of the middle Pleistocene, and is considered to belong to the immigrants of the second land connection (0.43 Ma) (Figure 21).

The geologic age of the Matsugae fauna has been problematic. Naora (1954) estimated the age of the fauna as early Pleistocene based on the mammal fauna. However, the Matsugae fauna is said to include both *Stegodon orientalis* and *Palaeoloxodon naumanni* (Proboscidea) according to Naora (1954).

This evidence may suggest that in the Matsugae fauna the two taxa coexisted, implying that the age of the fauna is near the boundary between QM4 and QM5. In contrast, this disagreement may be due to misidentification of the fossil specimens. We cannot confirm the identifications of these proboscidean fossils because the specimens have been lost.

Therefore, in this paper we estimate the age of the Matsugae fauna by means of biostratigraphic comparisons with other contemporaneous faunas of Japan using the entire mammalian fauna (Table 9).

The Matsugae fauna is correlated to the following Japanese faunas of the middle part of the middle Pleistocene (QM4): Table 9 shows a comparison of mammalian elements of the middle Pleistocene faunas on the Japanese Islands, such as the Matsugae fauna; the Bisan-Seto sea bottom assemblage in the Seto Island Sea, west Japan (Hasegawa, 1972; Otsuka, 1989); the Ikumo quarry fauna in Yamaguchi Prefecture, west Japan (Hasegawa, 1980); and the Lower Kuzuü fauna in Tochigi Prefecture, east Japan (Shikama, 1949).

The Matsugae fauna and Bisan-Seto sea bottom assemblage share *Panthera*, *Cervus*, *Palaeoloxodon*, and *Stegodon*. But the Bisan-Seto sea bottom assemblage is acervuline and comes from several sea and land areas, so that the correlation is tentative. The Matsugae fauna and Ikumo quarry fauna share *Apodemus*, *Microtus*, *Mustela*, *Cervus*, *Sus*, the Rhinocerotidae, and *Stegodon.* The Matsugae fauna and the Lower Kuzuü fauna share 12 genera (Table 9). Unlike the Ikumo quarry fauna, the Lower Kuzuü fauna lacks *Apodemus* and *Stegodon*.

In addition, the Matsugae fauna was compared with the Asian continental fauna. All the taxa of the Matsugae fauna are comparable to the middle Pleistocene northern Chinese Locality 1 of the Choukoutien fauna (Young, 1934). Ogino and Otsuka (2005) inferred that *Macaca* cf. *fuscata* of the Matsugae fauna is comparable in size and morphology to the middle Pleistocene northern Chinese *M. andersoni* and *M. robusta*. Ogino and Otsuka (2008) mentioned that *Oriensictis nipponica* of the Matsugae fauna is morphologically closely related to *O. melina* from Locality 1 of the Choukoutien fauna. The large-sized type of *Sus scrofa* of the Matsugae fauna is comparable to the Pleistocene northern Chinese large form of *S. scrofa*, such as "*S. lydekkeri.*"

The Matsugae fauna possesses several extinct species, such as *Microtus epiratticepoides*, *Cuon* sp., *Oriensictis nipponica*, *Panthera* sp., and *Dicerorhinus* sp. Extant taxa such as *Lepus* sp.*,* *Meles* sp., *Sus scrofa,* *Cervus* sp., and *Macaca* cf. *fuscata* in the Matsugae fauna are present on the Japanese main islands. However, these taxa in the Matsugae fauna exhibit their own unique dental characteristics. These characteristics can be regarded as due to processes of phyletic differentiation from relatives in Locality 1 of the Choukoutien fauna to Japanese forms. Notably, middle-sized mammals in the Matsugae fauna such as *Meles*, *Sus*, and *Macaca* show a marked tendency to be more derived and larger than the extant Japanese mammals.

As is the case with the other faunas of QM4, such as Ikumo and Lower Kuzuü, the Matsugae fauna falls at the lower limit of *Apodemus argenteus*, *Lepus*, *Mustela itatsi*, *Meles*, *Sus scrofa*, and *Macaca* (Figure 21). These taxa have a close relationship to northern Chinese Locality 1 of the Choukoutien fauna. This indicates that the presence of these taxa in Japan is due to immigration from the Asian continent after 0.43 Ma. At the same time, QM4 is also the upper limit of Rhinocerotidae and the lower limit of several extant taxa. Neither taxon is a confirmed index fossil, but their cooccurrence strongly supports placing the Matsugae fauna in biozone QM4 (Figure 21). However, *Apodemus speciosus* was discovered from QM3 of the Kobiwako Group (Kinki district, central Honshu Island) (Kawamura, 1989). It should be admitted as a relic of QM3 as a special case. Most of the taxa in the Matsugae fauna except for *Apodemus speciosus* can be considered as originating from northern China and immigrating from the Asian Continent to the Japanese Islands via the Korean Peninsula in the second land bridge connection (0.43 Ma).

Thus the faunal elements can be arranged into four categories (Table 1): the first comprises a mammal that existed in the Japanese mainland before QM4 (*Apodemus speciosus*); the second comprises mammals that are known only from QM4 (*Cuon* sp., *Oriensictis nipponica*, *Dicerorhinus* sp.); the third includes those that have specific characteristics of this period but may have a phyletic relationship to later Japanese mammals (*Microtus epiratticepoides, Lepus* sp., *Meles* sp., *Panthera* sp., *Cervus* sp., *Sus scrofa*, and *Macaca* cf. *fuscata*); and the fourth includes the direct ancestors of modern Japanese endemic species (*Apodemus argenteus* and *Mustela itatsi*). It should be noted that most of the taxa belonging to the second and the third categories are spatiotemporally confined by comparison with other middle Pleistocene Japanese mammal faunas. This fact might be explained by these taxa being under the strong influence of the continental element.

Although the Matsugae fauna cannot be placed with certainly into a Japanese Quaternary Mammal zone on the basis of the proboscideans, overall faunal resemblance strongly suggests the age of Matsugae fauna is in QM4. The cooccurrence of different categories suggests that the Matsugae fauna is one of the representative assemblages of the transitory immediately after the second land bridge connection event during QM4.

Acknowledgments

We are indebted to Hideo Nakaya, Kimihiko Oki, and Seiki Yamane from Kagoshima University and Masanaru Takai from Kyoto University who gave us valuable advice. We are grateful to Naoko Egi of Kyoto University for constructive comments on an earlier draft of this paper. We thank the following persons for the loan of specimens and assistance while visiting collections in their care; Didier Berthet (Muséum d'Histoire Naturelle de Lyon), Anne-Marie Bodergat, Abel Prieur (Université Lyon 1), Jerry Hooker (Natural History Museum, London) and Jin Chang-Zhu (Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing). Special thanks are due to the reviewers, Martin Pickford of the Collège de France and Takehisa Tsubamoto from the Center for Paleobiological Research, Hayashibara Biochemical Laboratories, Inc. This research was supported by the Sanshu Club Overseas Research Grant (2004) and the Sasakawa Scientific Research Grant from the Japan Science Society (2005).

References

Abe, H., 2000: *Illustrated Skulls of Japanese Mammals*, 279 pp. Hokkaido University Press, Sapporo.

Baskin, J. A., 1998: Mustelidae. *In*, Janis, C. M., Scott, K. M., and Jacobs, L. L. *eds*., *Evolution of Tertiary Mammals of North America. vol. 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*, p. 152–173. Cambridge University Press, Cambridge.

Billia, E. M., 2008: Revision of the fossil material attributed to *Stephanorhinus kirchbergensis* (Jäger 1839) (Mammalia, Rhinocerotidae) preserved in the museum collections of the Russian Federation. *Quaternary International*, vol. 179, p. 25–37.

Blanford, W. T., 1888: *The Fauna of British India Including Ceylon and Burma. Mammalia, Part 1*, 250 p. Taylor and Francis, London.

Blyth, E., 1875: Catalogue of the mammals and birds of Burma. *Journal of the Asiatic Society of Bengal*, vol. 44 (extra no. 2), pp. 1–167.

Brisson, M. J., 1762: *Regnum animale in classes IX distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem divisionem in ordines, sectiones, genera & species*, 296 p. Leiden.

Burmeister, H., 1850: *Verzeichnis der im Zoologischen Museum der Universität Halle-Wittenberg aufgestellten Säugethiere, Vögel, und Amphibien.* Friedrichs-Universität, Halle, 84 p.

Fooden, J., 1976: Provisional classifications and key to living species of macaques (Primates: *Macaca*). *Folia Primatologica*, no. 25 (2-3), p. 225–236.

Fujita, M., 2001: *Quaternary Wild Boars of Japan.* Ph.D. Thesis of Osaka Prefecture University, 124 p.

Fujita, M. and Kawamura, Y., 2001: Middle and Late Pleistocene wild boar remains from Locality 1 of Ube Kosan quarry in Yamaguchi Prefecture and from the Kannondo cave site in Hiroshima Prefecture, Western Japan. *Quaternary Research*, vol. 40, p. 149–160.

Fujita, M., Kawamura, Y., and Murase, N., 2000: Middle Pleistocene wild boar remains from NT Cave, Niimi, Okayama Prefecture, west Japan. *Journal of Geosciences, Osaka City University*, vol. 43, art. 4, p. 57–95.

Gloger, C. W. L., 1841: *Gemeinnütziges Hand- und Hilfsbuch für Naturgänger*, 495 p. Aug. Schulz & Co., Breslau.

Harunari, H., 2008: Matsugae specimens. *In*, Harunari, H. *ed*., *NAORA Nobuo Collection of Paleontological, Paleobotanical and Archaeological Objects and Related Documents. Catalogue of National Museum of Japanese History*, vol. 7, p. 24–28, 58–59. (*in Japanese*)

Hasegawa, Y., 1972: The Naumann' *Palaeoloxodon naumanni* (Makiyama) from the Late Pleistocene off Shakagahana, Shodoshima Is., in Seto Inland Sea, Japan. *Bulletin of the National Science Museum, Tokyo*, no. 15(3), p. 513–591.

Hasegawa, Y., 1980: Research history of mammalian assemblage of Akiyoshidai. *In*, Kohno, M. *ed*., *Calcareous cave of Akiyoshidai*. Memorial Issue on the Occasion of the Retirement of Professor Kohno Michihiro, 256 p. (*in Japanese*)

Hodgson, B. H., 1838: A classified catalogue of Nepalese Mammalia. *Annals and Magazine of Natural History*, vol. 11, p. 152–154.

Jäger, G. F., 1835–39: *Über die fossilen Säugetiere welche in Würtemberg in verschiedenen Formationen aufgefunden worden sind, nebst geognostischen Bemerkungen über diese Formationen.* C. Erhard Verlag, Stuttgart.

Kamei, T., Kawamura, Y. and Taruno, H., 1988: Mammalian stratigraphy of the Late Neogene and Quaternary in the Japanese Islands. *Journal of the Geological Society of Japan (Chishitsugaku-ronshu)*, vol. 30, p. 181–204.

Kaup, J., 1829: *Skizzirte Entwickelungs-Geschichte und natürliches System der Europäischen Thierwelt*, 154 p. Darmstadt.

Kawamura, Y., 1979: On the micro-mammalian faunal change since the Late Pleistocene in Japan. *Mammalogy*, vol. 38, p. 29–48.

Kawamura, Y., 1988: Quaternary rodent faunas in Japanese Islands (part 1). *Memoirs of the Faculty of Science, Kyoto University, Series of Geology and Mineralogy*, vol. 53, p. 31–348.

Kawamura, Y., 1989: Quaternary rodent faunas in Japanese Islands (part 2). *Memoirs of the Faculty of Science, Kyoto University. Series of Geology and Mineralogy*, vol. 53, 235 p.

Kawamura, Y., 1991: Quaternary mammalian faunas in the Japanese islands. *Quaternary Research*, vol. 30, p. 213–220. (*in Japanese with English abstract*)

Kawamura, Y., 1998: Immigration of mammals into the Japanese Islands during the Quaternary. *Quaternary Research*, vol. 37, p. 251–257. (*in Japanese with English abstract*)

Konishi, S. and Yoshikawa, S., 1999: Immigration times of the two proboscidean species, *Stegodon orientalis* and *Palaeoloxodon naumanni*, into the Japanese Islands and the formation of land bridge. *Earth Science*, vol. 53, p. 125–134.

Kretzoi, M., 1942: Präokkupierte und durch ältere zu ersetzende Säugetiernamen. *Föltani Közlöny*, no. 72, p. 345–349.

Kuwayama, R., Ozawa, T. and Otsuka, H., 1998: Fossil red deer *Cervus elaphus* from the sea-floor of the East China Sea off Amakusa-shimoshima Island, southwestern Kyushu, Japan. *Paleontological Research*, vol. 1, p. 1–11.

Lacépède, B. G. E., 1799: *Tableau des divisions, sous-divisions, ordres et genres de Mammifères*, 18 p. Plassan, Paris.

Linnaeus, C., 1758: *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis. Editio decima, reformata*, 823 p. Laurentii Salvii, Holmiae (Stockholm).

Montgelard, C., Catzeflis, F. and Douzery, E., 1997: Phylogenetic relationships of artiodactyls and cetaceans as deduced from the comparison of cytochrome b and 12S rRNA mitochondrial sequences. *Molecular Biology and Evolution*, vol. 14, p. 550–559.

Murray, A., 1866: *The Geographical Distribution of Mammals*, 420 p. Day and Son, Ltd., London.

Nakae, S., Ozaki, M., Ota, M., Yabumoto, Y., Matsuura, H. and Tomita, S., 1998: Geology of the Kokura district. Geological Survey of Japan. Fukuoka (14), no. 34, 126 p. (*in Japanese with English abstract*)

Naora, N., 1944:. *The History of Japanese Mammals.* Yotoku-sha, 265 p. (*in Japanese*)

Naora, N., 1954: Old Stone Age in Japan. *Archaeology Report of the Waseda University, Nara-Shobo*, vol. 2, 298 p. (*in Japanese*)

Naora, N., 1958: On the fossils of wild red dog in Japan. *Memoirs of the School of Science and Engineering, Waseda University*, vol. 10, p. 53–59. (*in Japanese*)

Naora, N., 1968: The fossils of otters discovered in Japan. *Memoirs of the School of Science and Engineering, Waseda University*, vol. 32, p. 1–11.

Naora, N., appended by Harunari, H., 1997: *Fossil Deer from Japan and its Vicinity*, 294 p. (*in Japanese*)

Naora, N., appended by Harunari, H., 1999: Osteology and ecology of badger from Pleistocene to the Present in Japan. *Dobutsu-Kokogaku*, vol. 13, p. 79–130. (*in Japanese*)

Ogino, S. and Otsuka, H., 2005: Morphological study of fossil *Macaca* cf. *fuscata* detected in the Middle Pleistocene Matsugae Fauna excavated from the cave deposits in northern Kyushu, Japan. *Primate Research*, vol. 21, p. 1–9. (*in Japanese with English Abstract*)

Ogino, S. and Otsuka, H., 2008: New middle Pleistocene Galictini (Mustelidae, Carnivora) from the Matsugae cave deposits, northern Kyushu, West Japan. *Paleontological Research*, vol. 12, p. 159–166.

Okazaki, Y., 2006: Rhinocerotid fossils of the "Matsugae Cave," Moji, Kitakyushu. *Abstracts with Programs of the 2006 Annual Meeting of the Paleontological Society of Japan*, p. 15. (*in Japanese*)

Oken, L., 1816: *Lehrbuch der Naturgeschichte. Bd. 3, Zoologie*, 1270 p. August Schmid und Co., Jena.

Otsuka, H., 1989: Fossil deer assemblage from sea bottom of Bisan-Seto area with special reference to their stratigraphic positions (Pleistocene deer fauna in Seto inland Sea, par 3). *Reports of the Faculty of Science, Kagoshima University (Earth Science and Biology)*, no. 22, p. 55–87.

Otsuka, H. and Shikama, T., 1978: Fossil Cervidae from the Tou-kou-shan Group in Taiwan. *Reports of the Faculty of Science, Kagoshima University (Earth Science and Biology)*, no. 11, p. 27–59.

Pei, W. C., 1934: On the Carnivora from Locality 1 of Choukoutien, *Paleontologia Sinica, Ser. C*, vol.8, fasc. 1, p. 76–80.

Pei, W. C., 1940: The Upper Cave Fauna of Choukoutien, *Paleontologia Sinica*, *Ser. C*, vol. 10, p. 58–61.

Reig, O. A., 1957: Note préliminaire sur un nouveau genre de mustélidés fossiles du Pléistocène de la République Argéntine. *Mammalia*, vol. 20, p. 223–230.

Ringström, T., 1924: Nashörner der *Hipparion*-Fauna Nord-Chinas. *Palaeontologia Sinica*, *Ser. C*, vol. 1, fasc. 4, 156 p.

Saito, H., 1939: On Canidae fossils from Ku-Hshiang-Tung, Manchuria, and from Japan. *Report of the First Scientific Expedition to Manchoukuo*, *Sec*. 2, par 4, p. 1–18. (*in Japanese with English abstract*)

Shackleton, N. J., 1995: New data on the evolution of Pliocene climatic variability. *In*, Vrba, E. S., Denton, D. H., Partridge, T. C. and Burkle, L. H. *eds*., *Paleoclimate and Evolution with Emphasis on Human Origins*, p. 242–248. Yale University.

Schlosser, M., 1924: Fossil Primates from China. *Palaeontologia Sinica, Ser. C*, vol. 1, fasc. 2, p. 3–11.

Schrank, F. P., 1798: *Fauna Boica. Bd. 1, Abh. 1*, 720 p. Stein, Nürnberg.

Shigehara, N., Kaneko, H., and Iwamoto, M., 2002: The teeth of Japanese macaque (*Macaca fuscata*) from the archaeological sites. *Asian Paleoprimatology*, vol. 2, p. 21–36. (*in Japanese*)

Shikama, T., 1936: Fossil boar from Kokura. *Journal of Geological Society of Tokyo*, vol. 43, p. 647–659.

Shikama, T., 1949: The Kuzuü ossuaries. *Science Reports of the Tohoku University, ser. 2 (Geology)*, vol. 23, 209 p.

Shikama, T. and Hasegawa, Y., 1965: Fossil suid from Kurihama, Kanagawa Prefecture. *Science Reports of the Yokohama National University, Sec.* 2, no. 12, p. 37–43.

Shikama, T., Hasegawa, Y., and Okafuji, G., 1967: On a rhinocerid skull from Isa, Yamaguchi Prefecture, Japan. *Bulletin of National Science Museum*, vol. 10, p. 455–461.

Takamatsu, K., 1997: Osteological study on Amami-rabbit (*Pentalagus furnessi*). *Master's Thesis of Kagoshima University*, 108 p.

Teilhard de Chardin, P. and Pei, W. C., 1941: The fossil mammals from Locality 13 of Choukoutien. *Palaeontologia Sinica, New Ser. C*, vol. 11, p. 1–119.

Temminck, 1844: *In*, Siebold, P. F., *Fauna Japonica. Mammalia*, p. 34. A. Amz, Lugduni Batavorum (Leiden).

Temminck, 1845a: *In*, Siebold, P. F., *Fauna Japonica. Mammalia*, p. 52. A. Amz, Lugduni Batavorum (Leiden).

Temminck, 1845b: *In*, Siebold, P. F., *Fauna Japonica. Mammalia*, P. 51. A. Amz, Lugduni Batavorum (Leiden).

Tokunaga, S., 1931: Remains of the Pleistocene den dwellers in Honshu, Kyushu and Chosen. *Nippon Gakujyutsu Kyokai Hokoku*, vol. 6, p. 175–178. (*in Japanese*)

Young, C. C., 1932: On the Artiodactyla from the *Sinanthropus* Site at Choukoutien. *Palaeontologia Sinica*, *Ser. C*, vol. 8, fasc. 2, p. 5–15.

Young, C. C., 1934: On the Insectivora, Chiroptera, Rodentia and Primates other than *Sinanthropus* from Locality 1 at Choukoutien. *Palaeontologia Sinica*, *Ser. C*, vol. 8, fasc. 3, p. 1–139.

Zdansky, O., 1924: Jungtertiä. *Palaeontologia Sinica*, *Ser. C*, vol. 2, fasc. 1, p. 47–67.

Zdansky, O., 1928: Die Säugetiere der Quartärfauna von Chou-Kou-Tien. *Palaeontologia Sinica*, *Ser. C*, vol. 5, fasc. 4, p. 91–95.