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Quaternary Rodent Faunas in the Japanese Islands (Part 2)

By

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Contents (Continued)

Family **Muridae** GRAY, 1821

Key to the genera of the Japanese murids

Six murid genera such as *Apodemus, Tokudaia, Diplothrix, Rattus, Micromys* and *Mus* are known from the present Japan. Among these, the first four are recorded as fossils. The key based on dental characters is given below.

1. Posterostyle always present in M^1 and M^2; posterior cingulum usually present in the same teeth; medial anteroconid always present in M_1 2
— Posterostyle and posterior cingulum absent from M^1 and M^2; medial anteroconid also absent from M_1 3

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2. Size larger; molars remarkably hypsodont; M^1 with four roots; labial anterocone always absent from M^2; anterior lamina of M_1 trifolium-shaped, but usually more complicate than that of *Apodemus*; two buccal accessory cusps present in M_1; M_1 with two roots; labial anteroconid present in M_3. .... ***Tokudaia***

— Size medium to small; hypsodonty medium (crown height of molars much lower than that of *Tokudaia*); M^1 almost always three- or four-rooted; labial anterocone of M^2 variable; anterior lamina of M_1 trifolium-shaped; number of buccal accessory cusps usually more than that of *Tokudaia*; M_1 with two roots; labial anteroconid usually absent from M_3. .... ***Apodemus***

— Size small (smaller than *Apodemus*); crown height of molars slightly lower than that of *Apodemus*; general molar patterns somewhat more cuspidate than those of *Tokudaia* and *Apodemus*; cusps of each molar less swollen than those of the two genera; M^1 with five roots; labial anterocone present in M^2; anterior and middle laminas of M_1 easily connecting at their medial parts to form "X-pattern"; in M_1, medial anteroconid small and separated from the anterior lamina; buccal accessory cusps of M_1 slender and continuous; M_1 with three roots; labial anteroconid present in M_3; hitherto unknown as fossils. .... ***Micromys***

3. Size much larger; M^1 with five roots; M^3 and M_3 relatively large; "X-pattern" of M_1 not easily formed; one or two buccal accessory cusps present in M_1 (mostly one); one buccal accessory cusp in M_2; labial anteroconid usually present in M_3. 4

— Size much smaller; M^1 with three roots; M^3 and M_3 relatively small; "X-pattern" of M_1 easily formed; M_1 and M_2 without buccal accessory cusps; labial anteroconid absent from M_3; hitherto unknown as fossils. .... ***Mus***

4. Size remarkably large; M^3 with more complicate structure. .... ***Diplothrix***

— Size smaller; M^3 with simple structure. .... ***Rattus***

Genus *Apodemus* KAUP, 1829

Three species of the genus *Apodemus* are known from the present Japanese Islands. They are *A. speciosus* (TEMMINCK), *A. argenteus* (TEMMINCK) and *A. giliacus* (THOMAS). The first two species are also known as fossils, as described below. The last species is restricted to the present Hokkaido. As far as their body sizes are concerned, *A. speciosus* is the largest of the three, whereas *A. argenteus* is the smallest (Figs. 161–166).

These species have the following osteological and dental characters in common.

Characters

The size is medium to small in the Palaearctic murids.

The skull bears the general features of the murids without any modification (Fig. 171). The dorsal surface of the skull is smooth. The rostrum is generally elongated, but its relative length varies from species to species. The nasals gradually taper backward and reach the position of the anterior border of the orbit. The interorbital region is flattened, and has nearly the same width as the rostrum. The supraorbital or lateral ridges are absent or weak. The incisive foramina are slender and parallel-sided. They terminate somewhat anterior to the position of the anterior face of M^1.

The mandible also has no peculiar morphological modifications (Figs. 174 and 182). The lateral outline of the diastema gently ascends towards M_1. The mental foramen opens on the buccal face somewhat anterior to the anterior root of M_1. The symphyseal eminence is usually inconspicuous. The upper masseteric crest is absent. However the lower masseteric crest is well-defined and extends from the mental foramen to the base of the angular process. The lingual face of the horizontal ramus is rather smooth. The area between the alveoli and ascending ramus is relatively narrow and flat. The coronoid process is delicate and sharply pointed, and projects postero-dorsally. The mandibular incision is considerably shallow. The condylar process is rather low and has approximately the same height as the coronoid process. It also extends postero-dorsally. The posterior end of the incisor forms a protuberant area on the buccal face of the ascending ramus. It is nearly as high as the occlusal surface of the lower molars. On the lingual face of the ascending ramus, a broad ridge formed by the capsule for the incisor extends from the area below the posterior root of M_3 to the mandibular foramen at the base of the condylar process. The angular process is not so elongated, but rather broadens dorso-ventrally. Its posterior end is rather obtuse, and situated anterior to the posterior tip of the condylar process. The lingual face of the angular process is broadly concave.

The upper and lower incisors are normal without any groove on their anterior faces. The molars are relatively delicate.

M^1 is composed of three chevrons (or laminas). Each of them comprises three cusps. The labial anterocone and posterostyle are always well developed. The prestyle and precingulum are mostly lacking. The degree of the development of the posterior cingulum is variable. The number of roots ranges from three to five.

M^2 comprises one antero-lingual cusp and two chevrons. Each chevron is composed of three cusps. An additional antero-buccal cusp (labial anterocone) is sometimes developed. The posterostyle is always well developed as in M^1. The degree of the development of the posterior cingulum is variable. The number of roots is three or four.

M^3 comprises one antero-lingual cusp, and two transverse or oblique laminas. The detailed pattern is variable from species to species. The number of roots is three.

M_1 is composed of three chevrons and one postero-central cusp. The most anterior chevron is trifolium-shaped. The accessory cusps on the buccal side is usually well-developed. The specific differences are very slight in the morphology of this tooth. The number of roots is mostly two, but very rarely three.

M_2 comprises two chevrons and one postero-central cusp. Additionally, the labial anteroconid is always present. The degree of the development of the accessory cusps on the buccal side is variable, but generally poorer than that of M_1. The specific differences are also slight in the morphology of this tooth. The number of roots is two.

M_3 comprises one anterior chevron and one posterior cusp. The labial anteroconid and other accessory cusps are usually absent. The morphology of the posterior cusp is specifically variable. The number of roots is two.

Key to the species of the Japanese *Apodemus*

1. Size smaller. Masseteric plate narrower; M^1 usually with four roots but rarely with five roots;

in M^1 and M^2, posterior cingulum well-developed, so that posterior cingulum-metacone connection as well as hypocone-metacone connection is easily formed (Fig. 160); M^2 with four roots and its labial anterocone well-defined; in M^3, two laminas arranged nearly parallel to transverse axis of crown; entoconid of M_3 somewhat elongated laterally. ....*A. **argenteus***

— Size larger. Masseteric plate broader; M^1 and M^2 with three roots; in M^3, two laminas arranged somewhat obliquely to the axis; entoconid of M_3 columnar in shape.................................... 2

2\. Size large. Rostrum longer; posterior border of nasal narrower; in M^1 and M^2, posterior cingulum less developed or absent, forming only a weak postero-buccal projection of hypocone, and never connecting with metacone; but the hypocone directly connecting with the metacone (Fig. 160); labial anterocone of M^2 poorly developed; occlusal outline of M^3 rounded; in M^3, anterostyle usually separated from protocone, but united in later stages of wear (Fig. 160). .... *A. **speciosus***

— Size medium. Rostrum shorter; posterior border of nasal broader; in M^1 and M^2, posterior cingulum usually connecting with metacone, but hypocone usually separated from metacone (Fig. 160); labial anterocone of M^2 well-developed; occlusal outline of M^3 somewhat elongated antero-posteriorly and triangular; in M^3, anterostyle easily connecting with protocone to form the most anterior additional lamina (Fig. 160). ....*A. **giliacus***

Some remarks on the classification of the Japanese fossil *Apodemus*

The fossils of *Apodemus* found in Japan can be easily classified into two forms by their size, namely larger and smaller ones. Both forms are usually coexistent in the fossil localities. Until recently, it was generally believed that only two species of *Apodemus, A. speciosus* and *A. argenteus*, were distributed in the present Japan. Such living species are decidedly different in size, as well as in external and osteological characters. From these facts, previous palaeontologists identified the larger and smaller fossil forms as *A. speciosus* and *A. argenteus* respectively. But such identification is quite insufficient, because the descriptions of the fossils were not given in most of

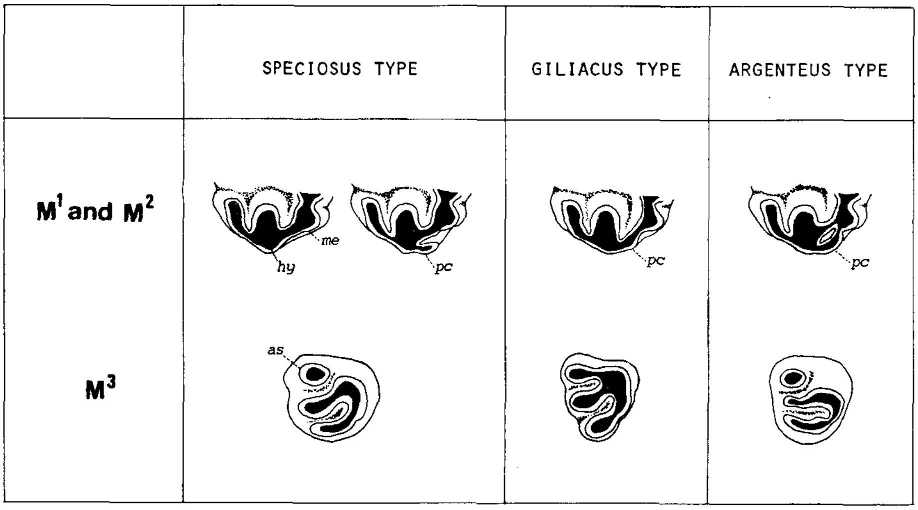


Fig. 160. Schematic diagram showing the morphological differences in the upper molars of the Japanese *Apodemus*. as, anterostyle; hy, hypocone; me, metacone; pc, posterior cingulum.

their works and thus the sufficient comparisons with living and fossil species were not carried out there. Additionally, the distribution of the third living species, *A. giliacus*, was recently discovered in Hokkaido (Kobayashi and Hayata, 1971). Therefore it is necessary to describe the fossil materials in detail, and to revise the previous classification of the fossils by comparing them with various living and fossil species including *A. giliacus*.

The author first investigated the differences in osteology, dental morphology and size among the three Japanese living species on the basis of numerous specimens. Subsequently, he examined the fossil materials, taking these differences into consideration, as well as comparing them with the continental living and fossil *Apodemus*. In regard to the molar sizes as shown in Figs. 161–166, *A. speciosus* is much larger than *A. argenteus*,

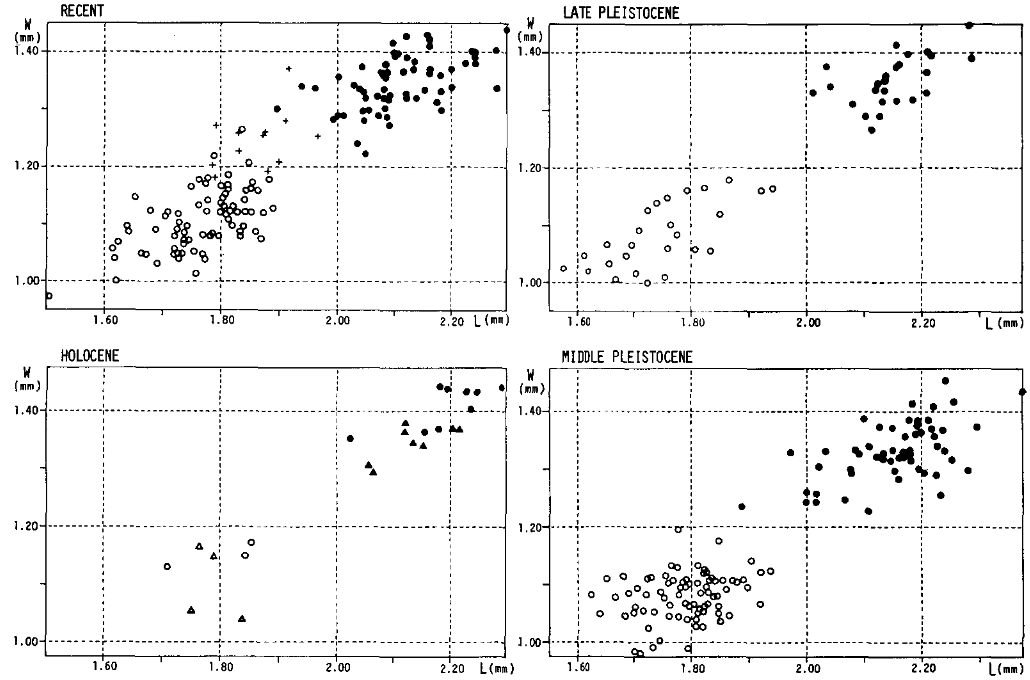


Fig. 161. Length and width plots of M^1 of the Japanese *Apodemus* showing the size variation in the populations of four different geological ages. Solid circle and triangle, *Apodemus speciosus*; cross mark, *A. giliacus*; open circle and triangle, *A. argenteus*. In the figure of "Recent" (left top), the data of *A. speciosus* and *A. argenteus* collected from Myogata, Gujohachiman, Mikawa Heights and Akiyoshi, and those of *A. giliacus* from Hokkaido (Kobayashi Collection) are plotted. The data of the fossil materials collected from the Holocene horizons of Kannondo Cave Site (open and solid circles) and Domen Cave Site (open and solid triangles) are plotted in the figure of "Holocene" (left bottom). Those from the Late Pleistocene horizons of Kannondo Cave Site are plotted in the figure of "Late Pleistocene" (right top). Those from Layers 1 and 3 of Locality 3 of Ube Kosan Quarry are plotted in the figure of "Middle Pleistocene" (right bottom).

but *A. giliacus* is intermediate between these two species in the living population. The measurements of the fossil materials are clearly divided into two clusters in the scatter diagrams of the Holocene, Late Pleistocene and Middle Pleistocene populations. These two clusters correspond to those of *A. speciosus* and *A. argenteus* of the living population, but the cluster corresponding to the living *A. giliacus* is absent from any fossil population. The fossil specimens belonging to the cluster with larger size are almost identical with the living *A. speciosus* in dental morphology. On the other hand, the molar patterns of the fossil specimens belonging to the cluster with smaller size are nearly the same as those of the living *A. argenteus.*

These facts indicate that all the fossils hitherto known from Japan should be identified as *A. speciosus* and *A. argenteus*, but *A. giliacus* is absent in any fossil population. Because the micro-mammalian fossil localities are restricted to Honshu, Shikoku and Kyushu, it can be said that *A. giliacus* has not invaded into these islands in any period since the Middle Pleistocene.

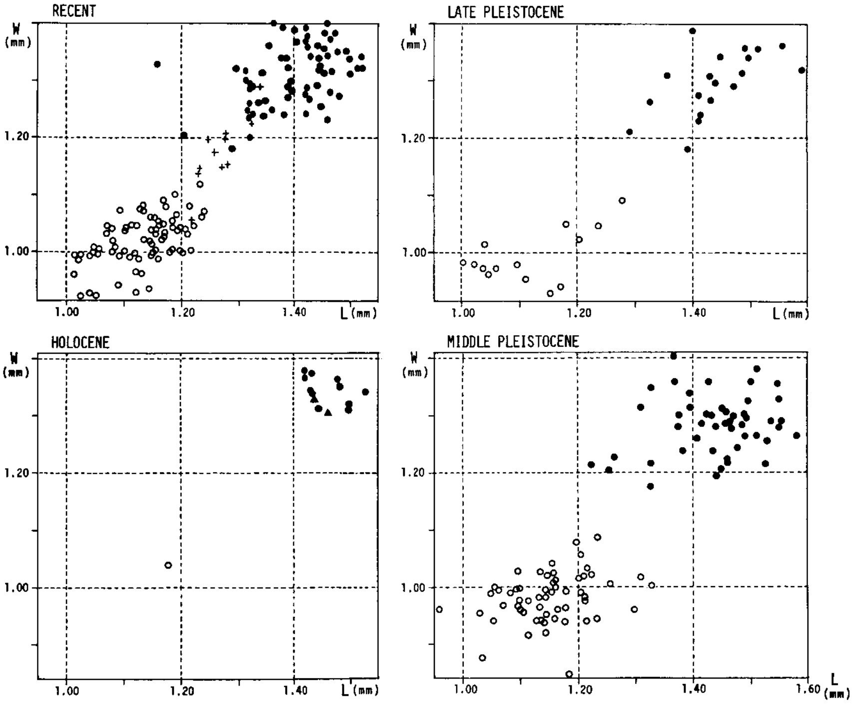


Fig. 162. Length and width plots of M^2 of the Japanese *Apodemus* showing the size variation in the populations of four different geological ages. Solid circle and triangle, *Apodemus speciosus*; cross mark, *A. giliacus*; open circle, *A. argenteus*. The data sources of each figure are the same as those of Fig. 161 (see the caption of Fig. 161).

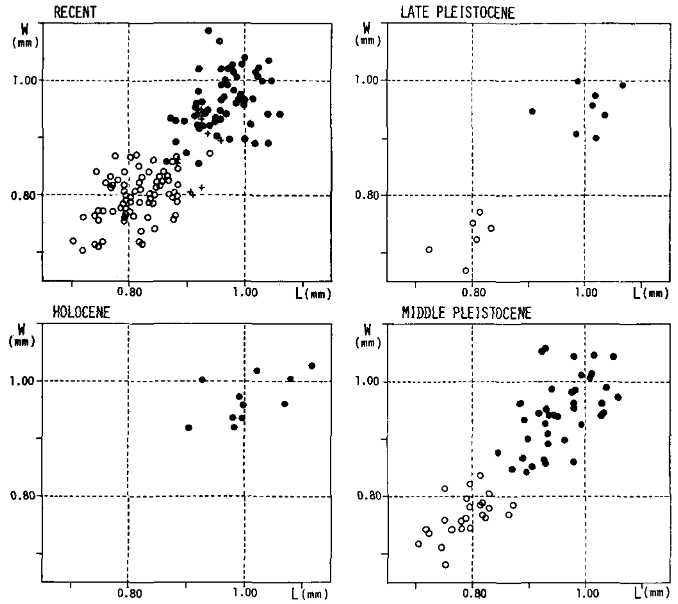


Fig. 163. Length and width plots of M^3 of the Japanese *Apodemus* showing the size variation in the populations of four different geological ages. Solid circle, *Apodemus speciosus*; cross mark, *A. giliacus*; open circle, *A. argenteus*. The data sources of each figure are the same as those of Fig. 161 (see the caption of Fig. 161).

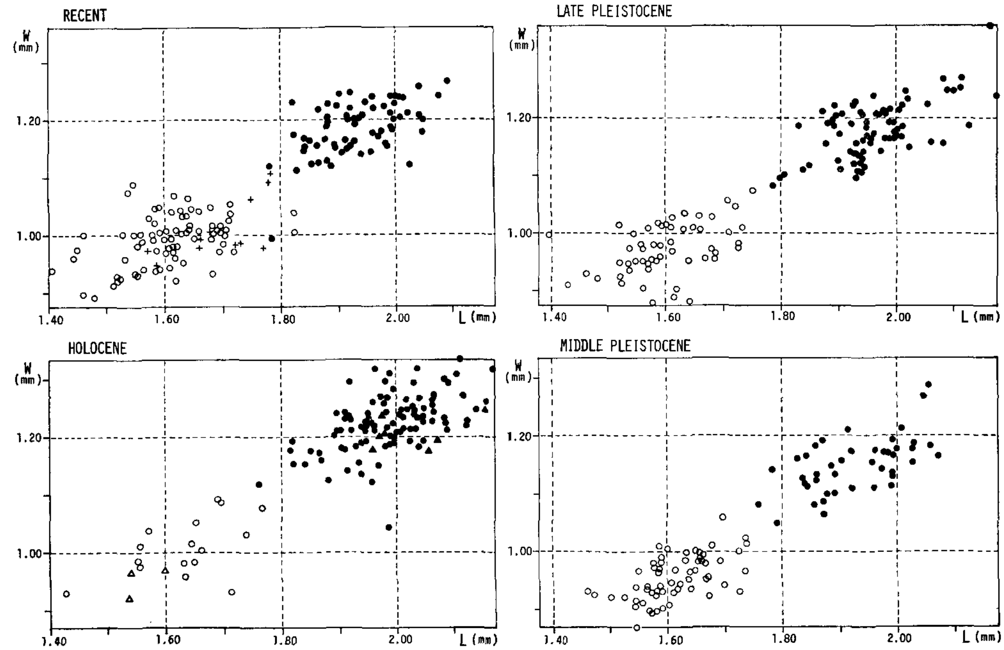


Fig. 164. Length and width plots of M_1 of the Japanese *Apodemus* showing the size variation in the populations of four different geological ages. Solid circle and triangle, *Apodemus speciosus*; cross mark, *A. giliacus*; open circle and triangle, *A. argenteus*. The data sources of each figure are the same as those of Fig. 161 (see the caption of Fig. 161).

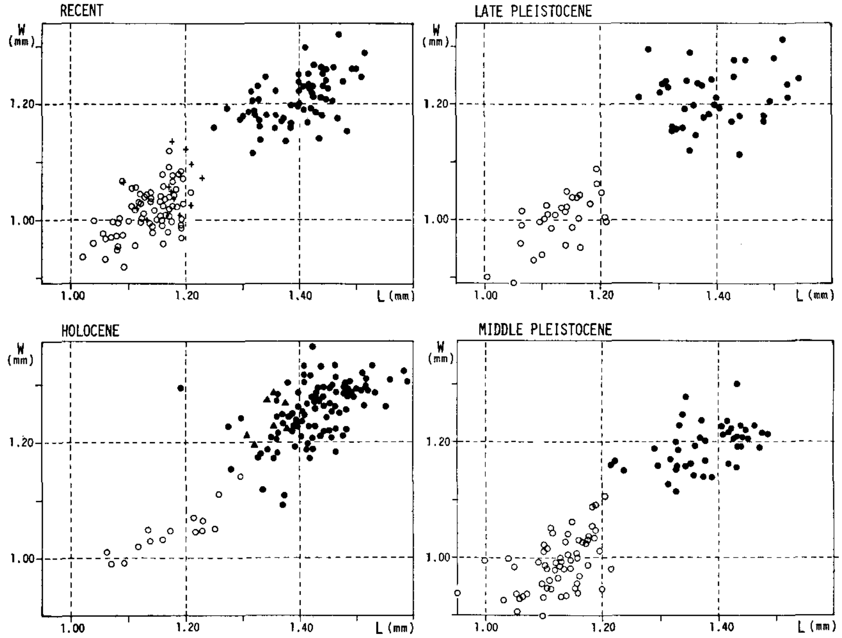


Fig. 165. Length and width plots of M_2 of the Japanese *Apodemus* showing the size variation in the populations of four different geological ages. Solid circle and triangle, *Apodemus speciosus*; cross mark, *A. giliacus*; open circle, *A. argenteus*. The data sources of each figure are the same as those of Fig. 161 (see the caption of Fig. 161).

The detailed descriptions of the osteological and dental characters of the present fossils are given in the subsequent sections. Moreover they are compared in detail with various living and fossil species of *Apodemus* there.

Geological and geographical distribution of fossil *Apodemus* in East Asia

The fossils of *Apodemus* are known from the Quaternary sediments of China, Korea and Japan in East Asia. Almost all the fossils from China have been assigned to *A. sylvaticus, A.* cf. *sylvaticus* or *A.* sp. except a few recent works (Tables 79 and 80). Previous authors believed that *A. sylvaticus* was widely distributed in the main part of China as a living species and they usually compared the Chinese fossil materials with the European *A. sylvaticus* or the Chinese living "*A. sylvaticus.*" However several recent authors regarded the Chinese "*A. sylvaticus*" as an independent species, *A. draco,* although the distribution of the true *A. sylvaticus* in the western extremities of China is generally accepted (CORBET, 1978; XIA, 1984 etc.). Therefore the previous identification of the Chinese fossils should be revised.

The Early Pleistocene murid faunas of East Asia are represented by the allied genera such as *Orientalomys* and *Chardinomys* instead of *Apodemus* (ZHENG, 1981; JACOBS

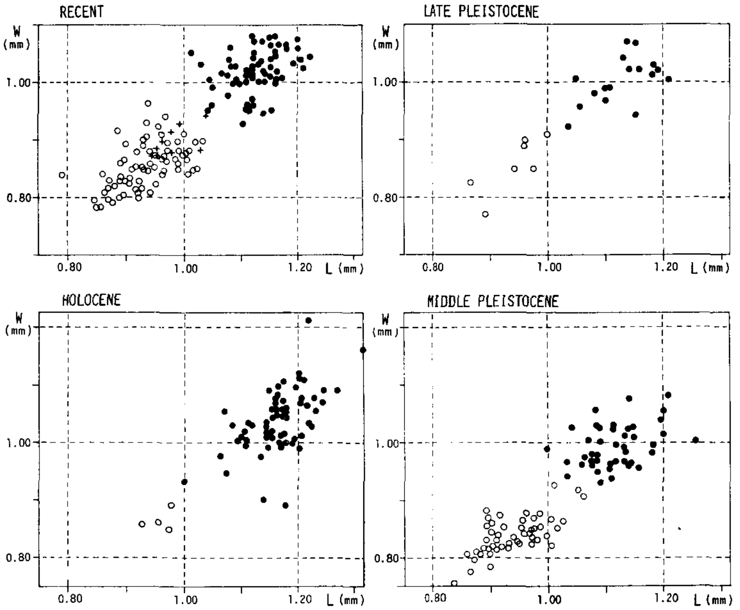


Fig. 166. Length and width plots of M_3 of the Japanese *Apodemus* showing the size variation in the populations of four different geological ages. Solid circle, *Apodemus speciosus*; cross mark, *A. giliacus*; open circle, *A. argenteus*. The data sources of each figure are the same as those of Fig. 161 (see the caption of Fig. 161).

and Li, 1982; Kawamura and Xue, 1984). Moreover *Parapodemus*, the direct ancestor of *Apodemus*, has been hitherto unknown from this area, although it was recorded from the Late Miocene sediments of Ertemte, Inner Mongolia (Schaub, 1938), and of Lufeng, Yunnan (Qiu *et al.*, 1985).

Teilhard (1940) described "*A.* cf. *sylvaticus*" from Huaiyu (Locality 18) near Peking (Fig. 167 and Table 79). It is the only Early Pleistocene record of *Apodemus* in East Asia. Its exact age is considered to be the later part of this period.

The Middle Pleistocene records of *Apodemus* are rather numerous (Fig. 168 and Table 79). They are known from the area around Peking to the course of the Yangtze River in China, and from west Japan and Korea. However they are absent from the northern areas such as Northeastern Provinces of China and USSR. Numerous fossils of *Apodemus* are obtained from Choukoutien (Localities 1, 2, 3 and 15). As regards the materials from Locality 1, two species, at least, seem to be present, although Young (1934) originally identified them as the single species, "*A. sylvaticus*." In Shaanxi Province, the fossils of *Apodemus* are recorded from Lantian (Gongwangling and Chenchiaou) and Luochuan. In the course of the Yangtze River, they are known from Hexian and Koloshan. The fossils from Hexian are identified as "*A. sylvaticus*"

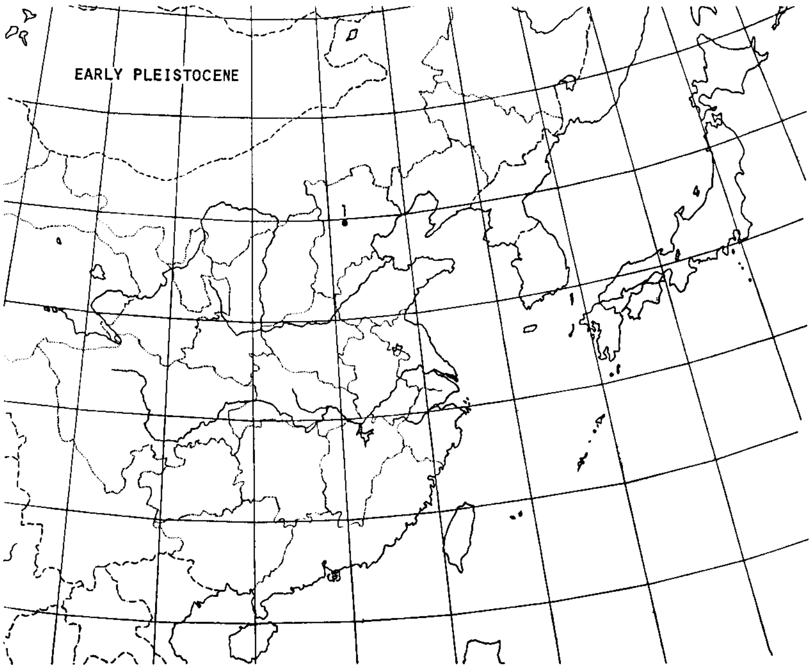


Fig. 167. Early Pleistocene fossil locality of *Apodemus* in East Asia. 1, Huaiyu. For detailed explanation see Table 79.

and *A. agrarius* (HUANG *et al.* 1982; ZHENG 1983), although their descriptions are not given in these papers.

The fossils of *Apodemus* are abundantly obtained from the Middle Pleistocene localities in Japan. They are referable to *A. speciosus* and *A. argenteus* which are considered to be the species endemic to the present Japan. Therefore these two species have undoubtedly inhabited in Japan since the Middle Pleistocene. It is interesting that there are no evidences on the invasions of the continental species of *Apodemus* (e. g. *A. agrarius, A. peninsulae* and *A. draco*) into the Japanese Islands except Hokkaido in any period since the Middle Pleistocene.

The Late Pleistocene fossil localities of *Apodemus* are rather few in China (Fig. 169 and Table 80). "*A. sylvaticus*" is known from three localities in or near Peking (Upper Cave of Choukoutien, Longgudong Cave and Yunshui Cave). Unfortunately, the descriptions of these fossils are quite insufficient. Recently, QIU *et al.* (1984) described *A. draco* and *A. latronum* from Sanjiacun in Yunnan Province. Their identifications are exceptionally based upon the current knowledge on the classification of the living *Apodemus*.

In contrast to China, the Late Pleistocene fossils of *Apodemus* are abundantly obtained from many localities in Japan (Fig. 169 and Table 80). They are exclusively

Fig. 168. Middle Pleistocene fossil localities of *Apodemus* in East Asia. 1, Ikumo Quarry; 2, Akiyoshi Area (Sumitomo Quarry, Ando Quarry, and Localities 1, 3 and 4 of Ube Kosan Quarry); 3, Matsugae Cave; 4, Sangwon Komunmoru Cave; 5, Choukoutien (Localities 1, 2, 3 and 15); 6, Luochuan; 7, Lantian (Gongwangling and Chenchiaou); 8, Hexian; 9, Koloshan. For detailed explanation see Table 79.

assignable to *A. speciosus* and *A. argenteus.* These two species are usually found altogether as in the Middle Pleistocene localities.

The Holocene records of *Apodemus* are lacking in China, as far as the available references to the present author are concerned. However they are rather numerous in Japan (Fig. 170 and Table 81). The Japanese *Apodemus* of this period is represented by *A. speciosus* and *A. argenteus* which are usually coexistent in each locality as in the Late Pleistocene.

The genus *Apodemus* is generally considered to be an inhabitant of forests and parklands in the temperate zone of Eurasia. In Japan, it is abundantly found in the fossil localities dated as the periods since the Middle Pleistocene, as already mentioned. This fact possibly indicates that the suitable habitats for *Apodemus* are continuously existent during the periods. Therefore it is roughly inferred that the climatic and vegetational conditions of the periods are generally temperate and sylvan, and not so different from the present conditions.

Table 79. Early and Middle Pleistocene fossil localities of *Apodemus* in East Asia. The numbers on the left side correspond to those in Figs. 167 and 168.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
EARLY PLEISTOCENE			
1. Huaiyu (Locality 18)	*Apodemus* cf. *sylvaticus*	Teilhard (1940)	
MIDDLE PLEISTOCENE			
JAPAN			
1. Ikumo Quarry	*Apodemus speciosus* *Apodemus argenteus*	Hasegawa (1963, 1966); Kowalski & Hasegawa (1976); this paper	
2. Sumitomo Quarry	*Apodemus speciosus*	Kowalski & Hasegawa (1976)	
2. Ando Quarry	*Apodemus speciosus* *Apodemus argenteus*	Hasegawa (1972); Kowalski & Hasegawa (1976)	
2. Locality 3 of Ube Kosan Quarry	*Apodemus speciosus* *Apodemus argenteus*	This paper	
2. Locality 1 of Ube Kosan Quarry	*Apodemus speciosus* *Apodemus argenteus*	This paper	
2. Locality 4 of Ube Kosan Quarry	*Apodemus speciosus* *Apodemus argenteus*	This paper	
3. Matsugae Cave at Tsunemi	*Apodemus speciosus*	Naora (1954)	
KOREA			
4. Sangwon Komunmoru Cave	*Apodemus sylvaticus*	Kim & Kim(1974)	
CHINA			
5. Locality 1 of Choukoutien	*Apodemus sylvaticus*	Zdansky (1928); Young (1934); Chao & Li (1960); Kahlke & Chow (1961)	Possibly assignable to at least two species.
5. Locality 2 of Choukoutien	*Apodemus sylvaticus*	Young (1927, 1932)	
5. Locality 3 of Choukoutien	*Apodemus sylvaticus*	Pei (1936)	
5. Locality 15 of Choukoutien	*Apodemus* sp.	Pei (1939)	No descriptions are given.
6. Luochuan	*Apodemus agrarius* *Apodemus* sp.	Liu & Yuan (1982); Kawamura & Xue (1984)	
7. Gongwangling at Lantian	*Apodemus* cf. *sylvaticus* *Apodemus* sp.	Hu & Qi (1978)	
7. Chenchiaou at Lantian	*Apodemus* cf. *sylvaticus*	Chow & Li (1965); Zhang *et al.* (1978)	
8. Hexian	*Apodemus sylvaticus* *Apodemus agrarius*	Huang *et al.* (1982); Zheng (1983)	No descriptions are given.
9. Koloshan	*Apodemus sylvaticus*	Young & Liu (1950)	

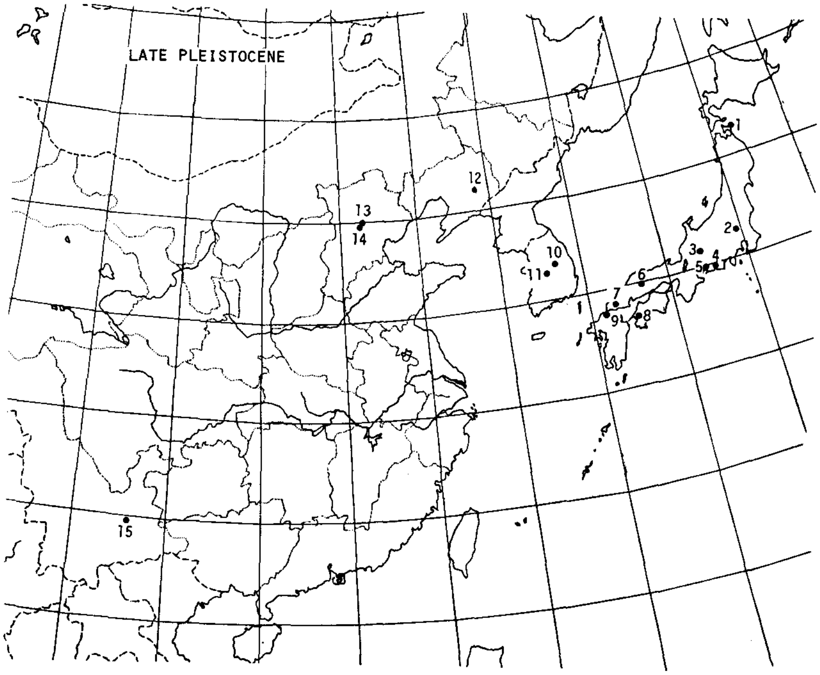


Fig. 169. Late Pleistocene fossil localities of *Apodemus* in East Asia. 1, Shiriya Quarry; 2, Kuzuü Area (Mizunoki Cave, Kadosawa, Miyata First Cave, Miyata Second Cave, Aisawa, Okubo, Yoshizawa Sekkai no. 8 Quarry, Yoshizawa Sekkai no. 10 Quarry, Tuidi, Komagata Sekkai Quarry, Maegawara Cave, Shimizu Sekkai Quarry, Takanosuzawa Cave, Takanosuzawa D Cave and Okada Quarry); 3, Sugi-ana Cave and Kumaishi-do Cave; 4, Shiraiwa Mine and Yage Quarry; 5, Suse Quarry and Ushikawa Mine; 6, Kannondo Cave Site; 7, Locality 2 of Ube Kosan Quarry; 8, Shikimizu Quarry; 9, Seiryukutsu Cave; 10, Chommal Yonggul Cave; 11, Turubong Cave; 12, Miaohoushan; 13, Longgudong Cave and Yunshui Cave; 14, Upper Cave of Choukoutien; 15, Sanjiacun. For detailed explanation see Table 80.

The fossil assemblages of *Apodemus* in Japan exclusively comprise the two species such as *A. speciosus* and *A. argenteus*, as already stated. The lack of the other species suggests that these two species are well adaptive to the environment of Japan and did not permit the invasions of the other species into Honshu, Shikoku and Kyushu, where the fossil localities are distributed. However it is assumed that the climate of Hokkaido has been colder and more continental than that of the other part of Japan, and this island has more frequently connected with the continent in cold periods of the Pleistocene. Therefore *A. giliacus* could invade from the continent and coexist with *A. speciosus* and *A. argenteus* there. Owing to the lack of the fossil localities in

Table 80. Late Pleistocene fossil localities of *Apodemus* in East Asia. The numbers on the left side correspond to those in Fig. 169.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
JAPAN			
1. Shiriya Quarry	*Apodemus speciosus* *Apodemus argenteus*	Nakajima (1958); Hasegawa (1966, 1972); Naora (1972); Kowalski & Hasegawa (1976)	Nakajima (1958) and Naora (1972) identified *A. argenteus* as *Mus* cf. *musculus molossinus*.
2. Mizunoki Cave	*Apodemus speciosus*	Naora (1954)	No descriptions are given; geological age uncertain.
2. Kadosawa (Tamasa Quarry)	*Apodemus speciosus*	Shikama (1937a, 1949)	No descriptions are given.
2. Miyata First Cave	*Apodemus speciosus* *Apodemus argenteus*	Shikama (1937a, 1949); Kowalski & Hasegawa (1976)	
2. Miyata Second Cave	*Apodemus speciosus* *Apodemus argenteus*	Shikama (1937a, 1949); Kowalski & Hasegawa (1976)	
2. Aisawa	*Apodemus speciosus* *Apodemus argenteus*	Kowalski & Hasegawa (1976); this paper.	
2. Okubo	*Apodemus speciosus*	Naora (1944)	No descriptions are given.
2. Yoshizawa Sekkai no.8 Quarry	*Apodemus speciosus*	Kowalski & Hasegawa (1976)	
2. Yoshizawa Sekkai no.10 Quarry	*Apodemus speciosus*	Naora (1954); Kowalski & Hasegawa (1976)	
2. Tuidi	*Apodemus speciosus*	Shikama (1937a, 1949); Naora (1944); Kowalski & Hasegawa (1976)	
2. Komagata Sekkai Quarry	*Apodemus speciosus*	Naora (1954)	No descriptions are given; geological age uncertain.
2. Maegawara Cave	*Apodemus speciosus*	Naora (1954)	No descriptions are given.
2. Shimizu Sekkai Quarry at Yamasuge	*Apodemus speciosus*	Naora (1954)	Ditto.
2. Takanosuzawa Cave	*Apodemus speciosus* *Apodemus argenteus*	Naora (1954); Kowalski & Hasegawa (1976)	
2. Takanosuzawa D Cave	*Apodemus speciosus*	Naora (1954)	No descriptions are given; geological age uncertain.
2. Okada Quarry (= Izurugahara Cave)	*Apodemus speciosus* *Apodemus argenteus*	Shikama (1937a, 1949); Naora (1944, 1954); Kowalski & Hasegawa (1976)	
3. Sugi-ana Cave	*Apodemus speciosus* *Apodemus argenteus*	Kawamura & Kajiura (1980); this paper	
3. Kumaishi-do Cave	*Apodemus speciosus* *Apodemus argenteus*	Kawamura & Ishida (1976); Kawamura (1977a); Okumura *et al.* (1982); this paper	
4. Shiraiwa Mine	*Apodemus speciosus* *Apodemus argenteus*	Hasegawa (1966); Kowalski & Hasegawa (1976).	
4. Yage Quarry	*Apodemus speciosus* *Apodemus argenteus*	Tomida (1978); this paper	
5. Suse Quarry (East Fissure)	*Apodemus speciosus* *Apodemus argenteus*	This paper	
5. Ushikawa Mine	*Apodemus speciosus* *Apodemus argenteus*	Kowalski & Hasegawa (1976)	

Table 80. (Continued)

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
JAPAN			
6. Kannondo Cave Site (Horizons M to P)	*Apodemus speciosus* *Apodemus argenteus*	Kawamura (1980, 1981, 1982); Kawamura *et al.* (1986); this paper	
7. Locality 2 of Ube Kosan Quarry	*Apodemus speciosus* *Apodemus argenteus*	This paper	
8. Shikimizu Quarry	*Apodemus speciosus* *Apodemus argenteus*	Shikama & Hasegawa (1962); Kowalski & Hasegawa (1976)	
9. Seiryukutsu Cave	*Apodemus argenteus*	Kawamura & Sotsuka (1984); this paper	
KOREA			
10. Chommal Yonggul Cave	*Apodemus sylvaticus*	Sohn (1984)	No descriptions are given.
11. Turubong Cave	*Apodemus agrarius* *Apodemus* sp.	Lee (1983); Sohn (1984)	Ditto.
CHINA			
12. Miaohoushan	*Apodemus sylvaticus*	Zhang *et al.* (1986)	No descriptions are given.
13. Longgudong Cave at Changping	*Apodemus sylvaticus*	Huang (1981)	Ditto.
13. Yunshui Cave	*Apodemus sylvaticus*	Huang & Hou (1984)	
14. Upper Cave of Choukoutien	*Apodemus sylvaticus*	Pei (1940)	
15. Sanjiacun	*Apodemus draco* *Apodemus latronum*	Qiu *et al.* (1984)	

Hokkaido, the history of these species remains unknown.

Apodemus speciosus (Temminck, 1844)

(Figs. 171–174)

Mus speciosus, Temminck 1844, *Fauna Japonica, Mamm.,* 52.

Synonym (*living forms*)——

Micromys speciosus Temminck; Thomas 1905, *Proc. Zool. Soc. London,* **1905**, 348–350, 358. (including *M. s. ainu* and *M. s. navigator*)

Apodemus speciosus Temminck; Thomas 1908, *Ibid.*, **1908**, 53.

Apodemus speciosus speciosus (Temminck et Schlegel), *A. s. ainu* (Thomas) and *A. s. navigator* (Thomas); Aoki 1915, *Nipponsan Nezumika* (*Japanese Muridae*), 31–40. (excluding *A. s. giliacus*)

Apodemus speciosus speciosus (Temminck), *A. s. ainu* (Thomas), *A. s. navigator* (Thomas) and *A. s. dorsalis* Kuroda; Kishida 1924, *Honyudobutsu Zukai* (*Monogr. Japanese Mamm.*), 116–120. (excluding *A. s. giliacus*)

Apodemus speciosus speciosus (Temminck et Schlegel) and *A. s. ainu* (Thomas); Watanabe 1937, *Occ. Pap. Ibaraki Agr. St.*, (2), 26–34.

Apodemus speciosus ainu (Thomas), *A. s. speciosus* (Temminck & Schlegel), *A. s. navigator* (Thomas) and *A. s. dorsalis* Kuroda; Kuroda 1940, *Monogr. Japanese Mamm.*, 121–125. (including *A. s.*, subsp. from Sado Island, but excluding *A. s. giliacus* and *A. s. peninsulae*)

Fig. 170. Holocene fossil localities of *Apodemus* in East Asia. 1, Tochibara Rockshelter Site; 2, Miwa Cave; 3, Suse Quarry; 4, Same Cave; 5, Kitoragawa Site; 6, Taishaku Area (Kannondo Cave Site, Anagami Rockshelter Site and Domen Cave Site); 7, Akiyoshi Area (Tanuki-ana Cave, Husen-ana Cave, Mizushimano-ana Cave, Irimino-ana Cave, Makurazino-ana Cave and Koziki-ana Cave); 8, Kurosegawa Cave; 9, Hirao-dai Area (Ohera-ana Cave, Ninjinkubo First Cave, Yakubono-ana Cave, Ojika-do Cave and Yoshigatani Third Cave); 10, Shimohieda Site; 11, Nodae-do; 12, Odong. For detailed explanation see Table 81.

Apodemus ainu ainu (THOMAS) and *A. speciosus* (TEMMINCK and SCHLEGEL); TOKUDA 1941, *Trans. Biogeogr. Soc. Japan*, **4**, 86–90. (including *A. speciosus* var. *navigator*, *A. s.* var. *tusimaensis*, *A. s.* var. *sadoensis* and *A. s.* var. *insperatus*, but excluding *A. ainu peninsulae*)

Apodemus sylvaticus speciosus (TEMMINCK), *A. s. ainu* (THOMAS), *A. s. insperatus* KURODA, *A. s. navigator* (THOMAS), *A. s. tusimaensis* TOKUDA, *A. s. sadoensis* TOKUDA and *A. s. dorsalis* KURODA; IMAIZUMI 1949, *Nat. Hist. Japanese Mamm.*, 257–260.

Apodemus speciosus TEMMINCK; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian Mammals*, 565.

Apodemus speciosus (TEMMINCK & SCHLEGEL); KURODA 1953, *Nippon Jurui Zusetsu* (*Monogr. Japanese Mamm.*), 85.

Apodemus speciosus TEMMINCK; IMAIZUMI 1960, *Coloured Illustr. Mamm. Japan*, 142–145.

Apodemus speciosus speciosus (TEMMINCK), *A. s. sadoensis* (TOKUDA), *A. s. navigator* (THOMAS), *A. s. insperatus* KURODA, *A. s. tusimaensis* TOKUDA, *A. s. dorsalis* KURODA, *A. ainu* (THOMAS) and *A. miyakensis* IMAIZUMI; IMAIZUMI 1969, *Bull. Nat. Sci. Mus. Tokyo*, **12**, 176–177.

Apodemus speciosus ainu (THOMAS); KOBAYASHI and HAYATA 1971, *Annot. Zool. Japon.*, **44**, 237–238.

Apodemus speciosus TEMMINCK; VORONTSOV *et al.* 1977, *Zool. Zhur.*, **56**, 444–445.

Table 81. Holocene fossil localities of *Apodemus* in East Asia. The numbers on the left side correspond to those in Fig. 170.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
JAPAN			
1. Tochibara Rock-shelter Site	*Apodemus speciosus* *Apodemus argenteus*	Miyao *et al.* (1980)	No descriptions are given.
2. Miwa Cave	*Apodemus speciosus* *Apodemus argenteus*	Miyao (1984)	Ditto.
3. Suse Quarry (West Fissure)	*Apodemus speciosus* *Apodemus argenteus*	This paper	
4. Same Cave	*Apodemus* sp.	Shikama *et al.* (1952)	No descriptions are given.
5. Kitoragawa Site	*Apodemus speciosus*	This paper	
6. Kannondo Cave Site (Holocene horizons)	*Apodemus speciosus* *Apodemus argenteus*	Kawamura (1978, 1979a); this paper	
6. Anagami Rockshelter Site	*Apodemus speciosus*	Kawamura (1983); this paper	
6. Domen Cave Site	*Apodemus speciosus* *Apodemus argenteus*	This paper	
7. Tanuki-ana Cave	*Apodemus speciosus* *Apodemus argenteus*	Shikama & Okafuji (1958); Kawamura & Tamiya (1980); this paper	
7. Husen-ana Cave	*Apodemus speciosus* *Apodemus argenteus*	This paper	
7. Mizushimano-ana Cave	*Apodemus speciosus* *Apodemus argenteus*	Shikama & Okafuji (1958)	No descriptions are given.
7. Irimino-ana Cave	*Apodemus argenteus*	Shikama & Okafuji (1958)	Ditto.
7. Makurazino-ana Cave	*Apodemus speciosus* *Apodemus argenteus*	Shikama & Okafuji (1958); Kowalski & Hasegawa (1976)	
7. Koziki-ana Cave	*Apodemus speciosus* *Apodemus argenteus*	Shikama & Okafuji (1958)	No descriptions are given.
8. Kurosegawa Cave	? *Apodemus argenteus* *Apodemus* sp.	Akazawa *et al.* (1976)	Ditto.
9. Ohera-ana Cave	*Apodemus speciosus*	Kawamura & Sotsuka (1984); this paper.	
9. Ninjinkubo First Cave	*Apodemus speciosus* *Apodemus argenteus*	Kawamura & Sotsuka (1984); this paper	
9. Yakubono-ana Cave	*Apodemus argenteus*	Kawamura & Sotsuka (1984); this paper	
9. Ojika-do Cave	*Apodemus argenteus*	Kawamura & Sotsuka (1984); this paper	
9. Yoshigatani Third Cave	*Apodemus speciosus* *Apodemus argenteus*	Kawamura & Sotsuka (1984); this paper	
10. Shimohieda Site	*Apodemus argenteus*	Hanamura (1985)	
KOREA			
11. Nodae-do	*Apodemus agrarius*	Sohn (1984)	No descriptions are given.
12. Odong	*Apodemus agrarius*	Sohn (1984)	Ditto.

Apodemus navigator Thomas; Vorontsov *et al.* 1977, *Ibid.*, **56**, 445–446.
Apodemus speciosus; Corbet 1978, *The Mammals of the Palaearctic Region*, 136.

Synonym (*fossil forms*)——

Apodemus sylvaticus speciosus; Naora 1954, *Old Stone Age in Japan*, 128–129; from Matsugae Cave.

Apodemus speciosus (Temminck); Shikama and Okafuji 1958, *Sci. Rep. Yokohama Nat. Univ.*, Sect 2, (7), 56, 58, 67–69; from Koziki-ana Cave, Makurazino-ana Cave and Mizushimano-ana Cave.

Apodemus speciosus speciosus (Temminck); Naora 1972, *Kodai-iseki Hakkutsu-no Sekitsui-dobutsu-itai* (*Vertebrate Remains from Archaeological Sites*), 178–179; from Shiriya Quarry.

Apodemus speciosus (Temminck); Kowalski and Hasegawa 1976, *Bull. Nat. Sci. Mus.*, Ser. C, **2**, 38–41; from Sumitomo Quarry, Ikumo Quarry, Ando Quarry, Shiraiwa Mine, Shiriya Quarry, Takanosuzawa Cave, Tuidi, Miyata (=Okubo) First Cave, Miyata (=Okubo) Second Cave, Okada Quarry, Nos. 8 and 10 Quarries of Yoshizawa Sekkai, Ushikawa Mine, Shikimizu Quarry and Makurazino-ana Cave.

Apodemus speciosus (Temminck); Kawamura and Ishida 1976, *Jour. Speleol. Soc. Japan*, **1**, 33; from Kumaishi-do Cave.

Apodemus speciosus (Temminck); Kawamura 1977, *Fossil Club Bull.*, (14), 7; from Kumaishi-do Cave.

Apodemus speciosus (Temminck); Kawamura 1978, 1979, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, **1**, 57; **2**, 46; from the Holocene horizons of Kannondo Cave Site.

Apodemus speciosus Temminck; Tomida 1978, *Bull. Mizunami Fossil Mus.*, (5), 127; from Yage Quarry.

Apodemus speciosus (Temminck); Kawamura and Tamiya 1980, *Bull. Akiyoshi-dai Mus. Nat. Hist.*, (15), 32; from Tanuki-ana Cave.

Apodemus speciosus (Temminck), Kawamura and Kajiura 1980, *Jour. Speleol. Soc. Japan*, **5**, 53; from Sugi-ana Cave.

Apodemus speciosus (Temminck); Kawamura 1981, 1982, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, **4**, 69; **5**, 60; from the Late Pleistocene horizons of Kannondo Cave Site.

Apodemus speciosus (Temminck); Okumura *et al.* 1982, *Earth Sci.*, **36**, 216; from Kumaishi-do Cave.

Apodemus speciosus; Kawamura 1983, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, **6**, 60; from Anagami Rockshelter Site.

Apodemus speciosus; Kawamura and Sotsuka 1984, *Bull. Kitakyushu Mus. Nat. Hist.*, (5), 172; from Ohera-ana Cave, Ninjinkubo First Cave and Yoshigatani Third Cave.

Apodemus speciosus (Temminck); Kawamura *et al.* 1986, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, **9**, 71; from the Late Pleistocene horizons of Kannondo Cave Site.

Materials——

MIDDLE PLEISTOCENE LOCALITIES

Ikumo Quarry

1 mandible with I (ASM 700012); 1 mandible without teeth (ASM 700013).

Locality 4 of Ube Kosan Quarry

22 isolated M^1 (ASM 701419–701430, 701521–701530); 12 isolated M^2 (ASM 701532–701540, 701616–701618); 7 isolated M^3 (ASM 701619–701624, 701650); 31 isolated M$_1$ (ASM 701651–701679, 701797, 701798); 23 isolated M$_2$ (ASM 701799–701816, 701921–701925); 13 isolated M$_3$ (ASM 701926–701937, 701991).

Locality 3 of Ube Kosan Quarry

Layer 1: 1 maxilla with M^1, M^2 and M^3 (KUJC 97170); 1 maxilla with M^1 and M^2 (KUJC 97169); 5 maxillae with M^2 and M^3 (KUJC97156, 97158, 97171, 97172, 97174); 1 maxilla with M^1 (KUJC97157); 3 maxillae with M^2 (KUJC97173, 97175, 97176); 1 maxilla with M^3 (KUJC97188); 2 maxillae without teeth (KUJC97258, 97259); 31 isolated M^1 (KUJC97162, 97198–97227); 16 isolated M^2 (KUJC97419–97434); 17 isolated M^3 (KUJC97549–97565); 1 mandible with I, M$_1$, M$_2$ and M$_3$ (KUJC97189); 1 mandible with I, M$_1$ and M$_2$ (KUJC 97159); 3 mandibles with M$_1$ (KUJC97160, 97161, 97190); 19 isolated M$_1$ (KUJC97164, 97632–97649); 17 isolated M$_2$ (KUJC97165–97167, 97813–97826); 24 isolated M$_3$ (KUJC 97934–97956, 97975).

Layer 3: 2 maxillae with M^2 (KUJC97263, 97264); 2 maxillae without teeth (KUJC97265, 97266); 25 isolated M^1 (KUJC97286–97308, 97349, 98047); 25 isolated M^2 (KUJC97459–97482, 98048); 25 isolated M^3 (KUJC97574–97597, 98049); 3 mandibles with I, M_1, M_2 and M_3 (KUJC97268, 97269, 97275); 2 mandibles with I, M_1 and M_2 (KUJC97276, 97277); 1 mandible with M_1 (KUJC97270); 2 mandibles with M_2 (KUJC97271, 97272); 2 mandibles with I (KUJC97273, 97274); 24 isolated M_1 (KUJC97676–97696, 97730–97732); 18 isolated M_2 (KUJC97846–97862, 97892); 16 isolated M_3 (KUJC97976–97991).

Layer 4: 1 fragmental skull with left M^1 (KUJC98057); 1 mandible with I (KUJC98058).

Layer 17: 1 maxilla with M^2 and M^3 (KUJC97350); 5 isolated M^1 (KUJC97355–97358, 97374); 5 isolated M^2 (KUJC97507–97511); 2 isolated M^3 (KUJC97612, 97613); 1 mandible with I, M_1, M_2 and M_3 (KUJC97352); 1 mandible with I, M_1 and M_2 (KUJC97351); 5 isolated M_1 (KUJC97733–97737); 3 isolated M_2 (KUJC97893–97895); 1 isolated M_3 (KUJC98023).

Layer 18: 17 isolated M^1 (KUJC97376–97378, 97388–97400, 98055); 23 isolated M^2 (KUJC 97515–97520, 97523–97539); 13 isolated M^3 (KUJC97615–97627); 23 isolated M_1 (KUJC 97750–97759, 97773–97784, 98056); 15 isolated M_2 (KUJC97901–97904, 97911–97921); 9 isolated M_3 (KUJC98026–98030, 98032–98035).

In addition to these materials, there are numerous unnumbered specimens such as maxillary fragments, mandibles and isolated teeth obtained from all the layers except Layer 7.

Locality 1 of Ube Kosan Quarry

Layer 4: 1 isolated M^2 (ASM 702069).

Layer 3: 1 isolated M^1 (ASM 702058); 4 isolated M^2 (ASM 702062, 702066–702068); 1 isolated M^3 (ASM 702063); 2 isolated M_1 (ASM 702056, 702064); 2 isolated M_2 (ASM 702057, 702065).

Layer 2: 2 isolated M^1 (ASM 702025, 702026); 2 isolated M^2 (ASM 702032, 702033); 3 isolated M^3 (ASM 702035–702037); 3 isolated M_1 (ASM 702038, 702039, 702054); 4 isolated M_2 (ASM 702042–702044, 702055); 3 isolated M_3 (ASM 702048–702050).

Layer 1: 1 isolated M^1 (ASM 702021); 3 isolated M_1 (ASM 702019, 702022, 702023); 1 isolated M_2 (ASM 702020).

LATE PLEISTOCENE LOCALITIES

Locality 2 of Ube Kosan Quarry

2 isolated M^1 (ASM 702070, 702071); 1 isolated M^3 (ASM 702072); 1 isolated M_1 (ASM 702073); 1 isolated M_2 (ASM 702074); 1 isolated M_3 (ASM 702075).

Aisawa Quarry

1 maxilla without teeth (KUJC100190); 1 isolated M^2 (KUJC100191); 1 mandible with M_1 (KUJC100192); 2 mandibles without teeth (KUJC100193, 100194); 1 isolated M_1 (KUJC100195); 3 isolated M_2 (KUJC100196–100198); 1 isolated M_3 (KUJC100199).

Sugi-ana Cave

1 maxilla with M^1, M^2 and M^3 (KUJC100200); 1 maxilla with M^1 and M^2 (KUJC100201); 1 maxilla with M^1 (KUJC100202); 1 maxilla with M^2 (KUJC100203); 2 maxillae with M^3 (KUJC100204, 100205); 47 maxillae without teeth (KUJC100206–100252); 35 isolated M^1 (KUJC 100253–100287); 9 isolated M^2 (KUJC100288–100296); 3 isolated M^3 (KUJC100297–100299); 3 mandibles with I, M_1, M_2 and M_3 (KUJC100300–100302); 2 mandibles with I, M_1 and M_2 (KUJC100303, 100304); 2 mandibles with M_1 and M_2 (KUJC100305, 100306); 3 mandibles with I and M_1 (KUJC100307–100309); 3 mandibles with I and M_2 (KUJC100310–100312); 1 mandible with M_1 (KUJC100313); 1 mandible with M_2 (KUJC100314); 10 mandibles with I (KUJC100315–100324); 34 mandibles without teeth (KUJC100325–100358); 34 isolated M_1 (KUJC100359–100392); 22 isolated M_2 (KUJC100393–100414); 3 isolated M_3 (KUJC100415–100417).

Yage Quarry

Site 2: 1 mandible with I, M_1, M_2 and M_3 (Matsuhashi Collection).

Site 4: 1 maxilla with M^2 and M^3 (Matsuhashi Collection); 1 isolated M^1 (KUJC100418); 2 mandibles with I, M_1, M_2 and M_3 (Matsuhashi Collection); 2 mandibles with I, M_1 and M_2 (Matsuhashi Collection); 1 mandible with M_2 (KUJC100419); 2 isolated M_1 (KUJC 100420, 100421); 1 isolated M_3 (KUJC100422).

Site 5: 2 isolated M^1 (KUJC100423, 100424).

Kannondo Cave Site (Late Pleistocene horizons; specimen numbers are prefixed by HUA)

Horizon P: 1 maxilla without teeth (K03795); 2 isolated M^1 (K03796, 03797); 2 isolated M^2 (K03798, 03799); 1 isolated M^3 (K03800); 1 mandible with M$_1$ and M$_2$ (K03801); 1 mandible without teeth (K03802); 6 isolated M$_1$ (K03803–03808); 3 isolated M$_2$ (K03809–03811).

Horizon O (lower part): 5 maxillae without teeth (K03812–03816); 5 isolated M^1 (K03817–03821); 3 isolated M^2 (K03822–03824); 4 isolated M^3 (K03825–03828); 1 mandible with M$_1$ and M$_2$ (K03829); 1 mandible with I (K03830); 6 mandibles without teeth (K03831–03836); 5 isolated M$_1$ (K03837–03841); 3 isolated M$_2$ (K03842–03844); 4 isolated M$_3$ (K03845–03848).

Horizon O (upper part): 1 maxilla with M^1 (K00277); 2 maxillae with M^2 (K00278, 00286); 2 maxillae without teeth (K00279, 00280); 6 isolated M^1 (K00281–00285, 00319); 3 isolated M^2 (K00287, 00288, 00320); 4 mandibles with M$_1$ and M$_2$ (K00289, 03849–03851); 1 mandible with I (K03852); 7 isolated M$_1$ (K00290–00296); 1 isolated M$_2$ (K00297); 2 isolated M$_3$ (K00298, 00299).

Horizon N: 3 maxillae without teeth (K00190, 00227, 00256); 2 isolated M^1 (K00206, 00207); 1 isolated M^2 (K00228); 4 mandibles with M$_1$ (K00208, 00223, 00257, 00258); 1 mandible with I (K00225); 7 mandibles without teeth (K00191, 00192, 00202, 00224, 00226, 00259, 00260); 17 isolated M$_1$ (K00196, 00197, 00203, 00229–00240, 00261, 00271); 5 isolated M$_2$ (K00198, 00221, 00241–00243); 5 isolated M$_3$ (K00204, 00222, 00244, 00245, 00262).

Horizon M (lower part): 2 maxillae with M^2 and M^3 (K00096, 00179); 2 maxillae with M^2 (K00099, 00100); 3 maxillae without teeth (K00097, 00098, 00101); 13 isolated M^1 (K00127–00135, 00158, 00164, 00173, 00174); 2 isolated M^2 (K00159, 00160); 1 mandible with I, M$_1$ and M$_3$ (K00105); 3 mandibles with M$_1$ and M$_2$ (K00110, 00166, 00180); 4 mandibles with M$_1$ (K00106, 00107, 00111, 00167); 1 mandible with M$_2$ (K00162); 11 mandibles without teeth (K00108, 00109, 00112–00117, 00163, 00172, 00181); 17 isolated M$_1$ (K00137–00145, 00161, 00165, 00168–00170, 00175, 00182, 00183); 10 isolated M$_2$ (K00149–00155, 00184, 00185, 00189); 2 isolated M$_3$ (K00157, 00186).

Horizon M (upper part): 1 maxilla with M^1, M^2 and M^3 (K00008); 1 maxilla with M^2 and M^3 (K00005); 1 maxilla with M^2 (K00001); 5 maxillae without teeth (K00002–00004, 00006, 00007); 7 isolated M^1 (K00055–00061); 3 isolated M^2 (K00064–00066); 2 mandibles with I, M$_1$, M$_2$ and M$_3$ (K00020, 00025); 1 mandible with I, M$_1$ and M$_2$ (K00019); 1 mandible with M$_1$ and M$_2$ (K00026); 2 mandibles with M$_1$ (K00053, 00054); 1 mandible with M$_2$ (K00027); 1 mandible with I (K00021); 6 mandibles without teeth (K00022–00024, 00028–00030); 17 isolated M$_1$ (K00068–00084); 5 isolated M$_2$ (K00086–00090); 4 isolated M$_3$ (K00091–00094).

In addition to these materials, numerous specimens such as maxillary fragments, mandibles and isolated teeth are also obtained from every horizon.

Kumaishi-do Cave

F$_3$: 1 maxilla with M^1, M^2 and M^3 (YKS 02015); 2 maxillae with M^2 and M^3 (YKS 02017, 02236); 3 maxillae with M^1 (YKS 02203, 02245, 02276); 1 maxilla with M^2 (YKS 02235); 2 maxillae with M^3 (YKS 02149, 02389); 58 isolated M^1 (YKS 02020–02026, 02028, 02030, 02059–02061, 02097–02099, 02109–2113, 02151, 02166, 02169, 02174, 02175, 02183, 02186–2189, 02191, 02213, 02214, 02227, 02228, 02247–02250, 02265–02268, 02278, 02282–02287, 02332–02338, 02380); 25 isolated M^2 (YKS 02041, 02042, 02052, 02075, 02115, 02118, 02124, 02209, 02221, 02235, 02237, 02238, 02272, 02273, 02280, 02303–02305, 02347–02351, 02382, 02383); 13 isolated M^3 (YKS 02054, 02263, 02275, 02324, 02325, 02331, 02363, 02366–02371); 2 mandibles with M$_1$, M$_2$ and M$_3$ (YKS 02127, 02244); 1 mandible with I, M$_1$ and M$_2$ (YKS 02281); 2 mandibles with M$_1$ and M$_2$ (YKS 02226, 02264); 1 mandible with M$_2$ and M$_3$ (YKS 02309); 2 mandibles with I and M$_2$ (YKS 02056, 02198); 2 mandibles with M$_1$ (YKS 02073, 02291); 3 mandibles with M$_2$ (YKS 02154, 02279, 02310); 1 mandible with I (YKS 02152); 2 mandibles without teeth (YKS 02150, 02163); 65 isolated M$_1$ (YKS 02032–02035, 02037–02040, 02064–02071, 02089–02091, 02093, 02094, 02107, 02108, 02117, 02145–02147, 02160, 02161, 02165, 02168, 02170, 02176, 02192–02195, 02205–02207, 02216, 02218, 02230–02233, 02246, 02253, 02269, 02270, 02277, 02292–02300, 02342, 02343, 02381, 02384, 02385); 39 isolated M$_2$ (YKS 02043–02045, 02047, 02048, 02051, 02076–02078, 02114, 02119–02123, 02130, 02157, 02159, 02197, 02199, 02210, 02222, 02239, 02258, 02259, 02271, 02311–02318, 02355–02358, 02386); 26 isolated M_3 (YKS 02053, 02057, 02058, 02079–02081, 02102, 02104, 02126, 02155, 02172, 02200, 02211, 02240–02242, 02262, 02326–02329, 02373, 02374, 02376, 02377, 02387).

F_1, F_2 and F_4: 1 maxilla without teeth (YKS 00425); 14 isolated M^1 (YKS 00400, 00403, 00405, 00408, 00414, 02009, 02010, 02082, 02084, 02138, 02139, 02142, 02177, 02179); 4 isolated M^2 (YKS 02005, 02014, 02088, 02105); 2 isolated M^3 (YKS 02135, 02182); 2 mandibles with I (YKS 00419, 00427); 6 mandibles without teeth (YKS 00420–00424, 00426); 18 isolated M_1 (YKS 00401, 00402, 00404, 00407, 00412–00414, 00416, 00417, 02000, 02006, 02011, 02013, 02085, 02086, 02129, 02134, 02144); 10 isolated M_2 (YKS 00409, 00411, 00415, 02003, 02083, 02136, 02143, 02178, 02180, 02184); 6 isolated M_3 (YKS 00410, 02004, 02007, 02012, 02087, 02185).

Suse Quarry (East Fissure; unnumbered specimens of the MATSUHASHI Collection)

1 skull fragment with left I, M^1 and M^2, and right I, M^1 and M^2; 3 mandibles with I, M_1, M_2 and M_3; 4 mandibles with I, M_1 and M_2; 1 mandible with I and M_1; 1 mandible with I.

HOLOCENE LOCALITIES

Suse Quarry (West Fissure; unnumbered specimens of the MATSUHASHI Collection)

1 skull fragment with left M^1, M^2 and M^3, and right M^1 and M^2; 1 maxilla with M^1, M^2 and M^3; 1 maxilla with M^2 and M^3; 1 maxilla with M^3; 2 maxillae without teeth; 12 mandibles with I, M_1, M_2 and M_3; 6 mandibles with I, M_1 and M_2; 3 mandibles with I and M_1; 1 mandible with M_2; 2 mandibles with I; 1 isolated M_1.

Kannondo Cave Site (Holocene horizons; specimen numbers are prefixed by HUA)

Horizon L: 1 maxilla without teeth (K03853); 11 mandibles with I, M_1, M_2 and M_3 (K03854–03864); 4 mandibles with I, M_1 and M_2 (K03865–03868); 2 mandibles with I (K03869, 03870); 2 mandibles without teeth (K03871, 03872).

Horizon K: 1 maxilla with M^1, M^2 and M^3 (K03873); 1 maxilla without teeth (K03874); 6 mandibles with I, M_1, M_2 and M_3 (K03875–03880); 1 mandible with M_1, M_2 and M_3 (K03881); 2 mandibles with I, M_1 and M_2 (K03882, 03883); 1 mandible with I, M_1 and M_3 (K03884); 1 mandible with I, M_2 and M_3 (K03885); 2 mandibles with M_1 and M_2 (K03886, 03887); 1 mandible with M_1 and M_3 (K03888); 1 mandible with M_2 and M_3 (K03889); 2 mandibles with I and M_2 (K03890, 03891); 1 mandible with M_2 (K03892); 1 mandible with I (K03893); 3 mandibles without teeth (K03894–03896); 2 isolated M_1 (K03897, 03898); 1 isolated M_2 (K03899); 1 isolated M_3 (K03900).

Horizon J: 1 maxilla with M^1, M^2 and M^3 (K03901); 1 maxilla with M^2 and M^3 (K03902); 1 maxilla without teeth (K03903); 7 mandibles with I, M_1, M_2 and M_3 (K03904–03910); 3 mandibles with M_1, M_2 and M_3 (K03911–03913); 7 mandibles with I, M_1 and M_2 (K03914–03920); 2 mandibles with M_1 and M_2 (K03921, 03922); 1 mandible with M_1 and M_3 (K03923); 3 mandibles with M_2 and M_3 (K03924–03926); 4 mandibles with I and M_1 (K03927–03930); 1 mandible with I and M_2 (K03931); 1 mandible with I and M_3 (K03932); 1 mandible with M_2 (K03933); 1 mandible with M_3 (K03934); 2 mandibles with I (K03935, 03936); 2 mandibles without teeth (K03937, 03938); 1 isolated M_3 (K03939).

Horizon I: 4 maxillae with M^1, M^2 and M^3 (K03940–03943); 1 maxilla with M^1 and M^2 (K03944); 3 maxillae with M^2 and M^3 (K03945–03947); 14 mandibles with I, M_1, M_2 and M_3 (K03948–03961); 9 mandibles with I, M_1 and M_2 (K03962–03970); 2 mandibles with I, M_2 and M_3 (K03971, 03972); 3 mandibles with M_1 and M_2 (K03973–03975); 1 mandible with M_2 and M_3 (K03976); 2 mandibles with I and M_1 (K03977, 03978); 2 mandibles with I and M_2 (K03979, 03980); 2 mandibles with M_1 (K03981, 03982); 1 mandible with M_2 (K03983); 2 mandibles with M_3 (K03984, 03985); 7 mandibles with I (K03986–03992); 4 mandibles without teeth (K03993–03996); 3 isolated M_1 (K03997–03999); 1 isolated M_2 (K04000); 1 isolated M_3 (K04001).

Horizon H: 2 mandibles with I, M_1, M_2 and M_3 (K04002, 04003); 1 mandible with I and M_1 (K04004).

Horizon F: 1 mandible with I, M_1, M_2 and M_3 (K04005).

Horizon unknown: 1 isolated M^1 (K04006); 1 isolated M^2 (K04007); 1 isolated M^3 (K04008);

3 mandibles with I, M_1, M_2 and M_3 (K04009–04011); 2 mandibles with M_1, M_2 and M_3 (K04012, 04013); 1 mandible with I, M_1 and M_2 (K04014); 2 mandibles with M_1 and M_2 (K04015, 04016); 1 mandible with I and M_2 (K04017); 2 mandibles with M_1 (K04018, 04019); 2 mandibles without teeth (K04020, 04021); 1 isolated M_1 (K04022); 2 isolated M_2 (K04023, 04024); 2 isolated M_3 (K04025, 04026).

Domen Cave Site (specimen numbers are prefixed by HUA)

Horizon V: 4 maxillae without teeth (D00082–00085); 4 isolated M^1 (D00086–00089); 2 isolated M^2 (D00090, 00091); 1 mandible without teeth (D00092); 8 isolated M_1 (D00093–00100); 8 isolated M_2 (D00101–00108).

Horizon unknown: 1 mandible with M_1 and M_2 (D00109); 2 isolated M_1 (D00110, 00111).

Tanuki-ana Cave

Layer 4: 1 maxilla with M^1, M^2 and M^3 (ASM 702076); 5 maxillae with M^1 and M^2 (ASM 702077–702081); 1 maxilla with M^2 and M^3 (ASM 702082); 7 maxillae with M^1 (ASM 702083–702089); 1 maxilla with M^2 (ASM 702090); 2 maxillae with M^3 (ASM 702091, 702092); 20 maxillae without teeth (ASM 702093–702112); 92 isolated M^1 (ASM 702113–702204); 44 isolated M^2 (ASM 702205–702248); 14 isolated M^3 (ASM 702249–702262); 1 mandible with M_1, M_2 and M_3 (ASM 702263); 1 mandible with I, M_1 and M_2 (ASM 702264); 3 mandibles with M_1 and M_2 (ASM 702265–702267); 9 mandibles with M_1 (ASM 702268–702276); 1 mandible with M_2 (ASM 702277); 2 mandibles with M_3 (ASM 702278, 702279); 26 mandibles without teeth (ASM 702280–702305); 77 isolated M_1 (ASM 702306–702382); 66 isolated M_2 (ASM 702383–702448); 32 isolated M_3 (ASM 702449–702480).

Layer 3: 1 maxilla with M^2 and M^3 (ASM 702481); 1 maxilla with M^2 (ASM 702482); 4 maxillae without teeth (ASM 702483–702486); 27 isolated M^1 (ASM 702487–702513); 9 isolated M^2 (ASM 702514–702522); 1 isolated M^3 (ASM 702523); 1 mandible with I, M_1, M_2 and M_3 (ASM 702524); 1 mandible with I, M_1 and M_2 (ASM 702525); 2 mandibles with M_1 and M_2 (ASM 702526, 702527); 1 mandible with M_1 (ASM 702528); 10 mandibles without teeth (ASM 702529–702538); 20 isolated M_1 (ASM 702539–702558); 10 isolated M_2 (ASM 702559–702568); 5 isolated M_3 (ASM 702569–702573).

Layers 3 to 2: 1 maxilla with M^2 and M^3 (ASM 702574); 3 maxillae with M^2 (ASM 702575–702577); 3 maxillae without teeth (ASM 702578–702580); 17 isolated M^1 (ASM 702581–702597); 8 isolated M^2 (ASM 702598–702605); 3 isolated M^3 (ASM 702606–702608); 1 mandible with M_1 (ASM 702609); 1 mandible with I (ASM 702610); 6 mandibles without teeth (ASM 702611–702616); 22 isolated M_1 (ASM 702617–702638); 8 isolated M_2 (ASM 702639–702646); 8 isolated M_3 (ASM 702647–702654).

Layer 2: 2 maxillae with M^1 and M^2 (ASM 702655, 702656); 1 maxilla with M^2 and M^3 (ASM 702657); 3 maxillae with M^1 (ASM 702658–702660); 2 maxillae with M^2 (ASM 702661, 702662); 12 maxillae without teeth (ASM 702663–702674); 51 isolated M^1 (ASM 702675–702725); 25 isolated M^2 (ASM 702726–702750); 3 isolated M^3 (ASM 702751–702753); 1 mandible with I, M_1, M_2 and M_3 (ASM 702754); 2 mandibles with M_1, M_2 and M_3 (ASM 702755, 702756); 2 mandibles with I, M_1 and M_2 (ASM 702757, 702758); 6 mandibles with M_1 and M_2 (ASM 702759–702764); 1 mandible with I and M_2 (ASM 702765); 7 mandibles with M_1 (ASM 702766–702772); 3 mandibles with M_2 (ASM 702773–702775); 1 mandible with M_3 (ASM 702776); 3 mandibles with I (ASM 702777–702779); 14 mandibles without teeth (ASM 702780–702793); 55 isolated M_1 (ASM 702794–702848); 31 isolated M_2 (ASM 702849–702879); 7 isolated M_3 (ASM 702880–702886).

Layer 1: 2 maxillae with M^1 (ASM 702887, 702888); 1 maxilla with M^2 (ASM 702889); 2 maxillae without teeth (ASM 702890, 702891); 5 isolated M^1 (ASM 702892–702896); 5 isolated M^2 (ASM 702897–702901); 2 isolated M^3 (ASM 702902, 702903); 1 mandible with M_3 (ASM 702904); 2 mandibles without teeth (ASM 702905, 702906); 9 isolated M_1 (ASM 702907–702915); 5 isolated M_2 (ASM 702916–702920).

Husen-ana Cave

1 maxilla with M^1 and M^3 (ASM 702987); 3 maxillae without teeth (ASM 702988–702990); 20 isolated M^1 (ASM 702921–702940); 6 isolated M^2 (ASM 702942–702947); 1 isolated M^3 (ASM 702948); 2 mandibles with I, M_1, M_2 and M_3 (ASM 702975, 702982); 1 mandible with M_1, M_2

and M_3 (ASM 702976); 1 mandible with I and M_1 (ASM 702977); 1 mandible with I and M_2 (ASM 702978); 3 mandibles with I (ASM 702979, 702983, 702984); 2 mandibles without teeth (ASM 702980, 702981); 13 isolated M_1 (ASM 702949–702961); 4 isolated M_2 (ASM 702966–702969); 2 isolated M_3 (ASM 702973, 702974).

Anagami Rockshelter Site (Grids A-1, B-0 and B-1)

1 mandible with M_1 and M_2 from Layer 6 (HUA-A00011); 1 mandible with I, M_1 and M_2 (HUA-A00012) and 1 mandible without teeth (HUA-A00013) from Layer 4; 1 maxilla with M^1 from Layer 3 (HUA-A00014).

Kitoragawa Site (unnumbered specimens)

1 isolated M^2; 1 mandible with M_1, M_2 and M_3; 1 isolated M_1.

Yoshigatani Third Cave (unnumbered specimen of the SOTSUKA Collection)

1 mandible with I, M_1, M_2 and M_3.

Ninjinkubo First Cave (unnumbered specimens of the SOTSUKA Collection)

1 fragmental skull with M^2; 1 isolated M^1; 1 mandible with I, M_1 and M_2; 2 mandibles with I; 2 isolated M_1; 1 isolated M_2; 1 isolated M_3.

Ohera-ana Cave (unnumbered specimen of the SOTSUKA Collection)

1 mandible with I.

Diagnosis

Size decidedly larger than that of *A. argenteus*. Rostrum remarkably elongated; anterior margin of masseteric plate situated considerably anterior to the upper border of infraorbital foramen in lateral view; lateral ridges rather weak; diastema of mandible relatively long.

Upper molars almost always with three roots; posterior cingulums of M^1 and M^2 much weaker than those of *A. argenteus*, and never connecting with metacone; labial anterocone of M^2 poorly developed or absent; length and width of M^1 usually more than 1.95 and 1.23 mm respectively; those of M^2 usually more than 1.28 and 1.19 mm respectively; two laminas of M^3 arranged somewhat obliquely to the transverse axis of the crown; length and width of M^3 usually more than 0.88 and 0.85 mm respectively. Lower molars with two roots each; length and width of M_1 usually exceeding 1.78 and 1.06 mm respectively; those of M_2 usually more than 1.25 and 1.09 mm respectively; entoconid of M_3 rather columnar in shape; length and width of M_3 usually more than 1.03 and 0.93 mm respectively.

Description

Skull——

The skull is few and fragmental in the present fossil materials. The anterior part of the skull is frequently preserved, but the braincase is always damaged (Fig. 171).

The general characters are well coincident with the generic characters. The rostrum is remarkably elongated and slender. The nasals gradually taper backwards, and their posterior margins are rather narrow. The masseteric plate broadens anteriorly, so that its anterior margin reaches the position considerably anterior to the upper border of the infraorbital foramen in lateral view. In dorsal view, the upper border of the foramen intrudes into the base of the zygomatic arch more deeply than in *A. argenteus*. The lateral ridges are relatively weak. The alveolar pits of M^1 on maxilla are almost always three in number. Those of M^2 and M^3 are also three

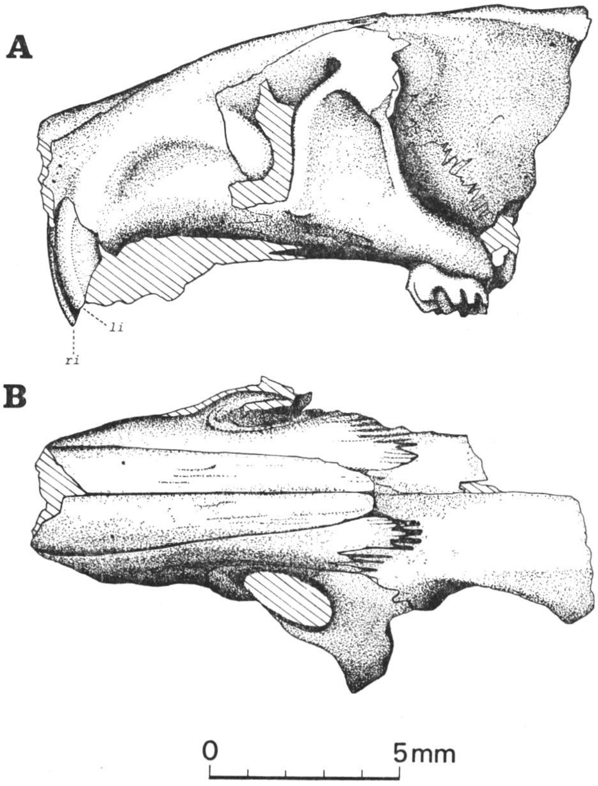


Fig. 171. *Apodemus speciosus.* Fragmental skull from Layer 4 of Locality 3 of Ube Kosan Quarry (KUJC98057). A, left lateral view; B, dorsal view; li, left incisor; ri, right incisor.

respectively (Fig. 172).

M^1——

The outline of the crown is oval in occlusal view. The crown comprises three transverse cusp rows which show a chevron-shape. Each chevron comprises three main cusps.

The anterior chevron is composed of the labial anterocone, lingual anterocone and anterostyle which are closely arranged in each other. The enteroconule is usually invisible. The lingual anterocone is situated in the centre of this chevron, and is much larger than the other two cusps. It is somewhat elongated laterally and inclined to the front. Its occlusal surface is readily connected with those of the labial anterocone and anterostyle even in early stages of wear, because the notches among these cusps are narrow and shallow (especially the notch between the lingual anterocone and labial anterocone disappears earlier). A weak precingulum is rarely found on the anterior face of the lingual anterocone. An accessory tubercle (prestyle) is also rarely

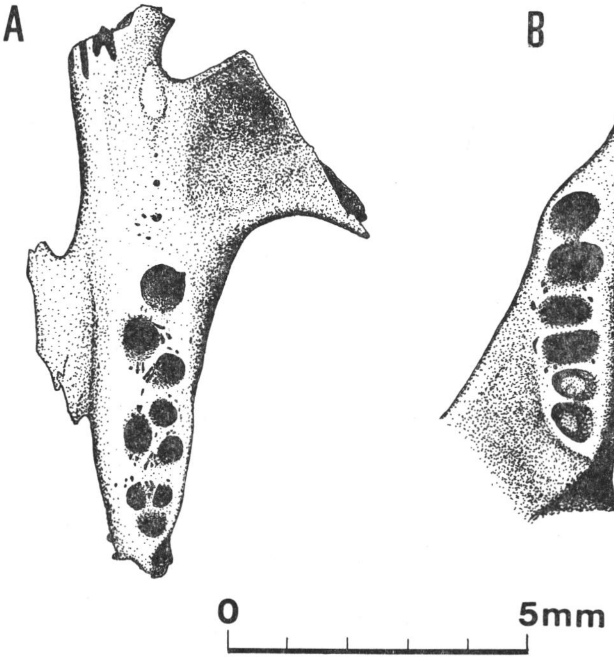


Fig. 172. *Apodemus speciosus.* Alveolar patterns on maxilla (A) and mandible (B). A, left maxilla from Layer 1 of Locality 3 of Ube Kosan Quarry (KUJC97258); B, left mandible with I from Layer 4 of the same locality (KUJC98058).

present on the antero-lingual or antero-buccal face of the same cusp. The frequencies of the appearances of the precingulum and prestyle are analysed in the next section.

The columnar-shaped labial anterocone is attached on the buccal face of the lingual anterocone. It is clearly inclined to the front. The anterostyle is also columnar in shape, and attached on the postero-lingual face of the lingual anterocone. It is almost erected. The relative position of the occlusal surface of the labial anterocone against that of the anterostyle is changeable in accordance with the wear of the crown owing to such three-dimensional structures of these two cusps. In early stages of wear, the occlusal surfaces of these cusps are opposite in position, or that of the anterostyle is slightly posterior to that of the labial anterocone. As the wear is advanced, the latter is remarkably shifted anteriorly. The posterior spur of the labial anterocone is sometimes observable, but is neither so well-developed nor frequently found as in *A. argenteus.* A similar spur is rarely observed on the posterior face of the anterostyle. The frequencies of the appearances of these spurs are analysed in the next section.

The valley between the anterior and middle chevrons is broad and deep, so that both chevrons are not confluent even in later stages of wear. An accessory cusp is very rarely observed on the lingual or buccal entrance of the valley. Only in ASM 702113 from Layer 4 of Tanuki-ana Cave, such a cusp is present on both lingual and buccal entrances.

The middle chevron comprises the paracone, protocone and enterostyle. The protocone is the largest central cusp in this chevron, and is located anterior to the other two lateral cusps. The inclination of the paracone to the front is somewhat gentler than that of the enterostyle. However the occlusal surfaces of these two cusps are set approximately in the same transverse line. The protocone-paracone connection on the occlusal surface is formed somewhat earlier than the protocone-enterostyle connection.

The valley between the middle and posterior chevrons is considerably deep. It opens buccally and lingually through the isthmuses between the paracone and metacone, and between the enterostyle and posterostyle respectively. Because the former isthmus is shallower and narrower than the latter, the occlusal surfaces of the paracone and metacone are easily confluent in earlier stages of wear. When the latter isthmus subsequently disappears, this valley becomes a closed pit surrounded by the ring which is formed by the cusps of the middle and posterior chevrons.

The posterior chevron comprises a large central cusp (hypocone) and two lateral cusps (metacone and posterostyle). The metacone is columnar in shape and somewhat inclined to the front. From this cusp, a distinct ridge extends postero-lingually to the hypocone. The posterostyle is well-defined, but smaller than the metacone. This cusp is somewhat elongated and can be sometimes regarded as a swelling of the ridge extending antero-lingually from the hypocone. The metacone and posterostyle are arranged in the opposite position.

The degree of the development of the posterior cingulum is quite variable, but decidedly weaker than that in *A. argenteus*. In some specimens, it is completely absent, or is only a faint spur on the postero-buccal face of the hypocone. In other specimens, it is well developed to form a small columnar tubercle attached on that face, but it is considerably lower than the hypocone when observed in early stages of wear. As the wear is advanced, its occlusal surface is elongated to be confluent with that of the hypocone. In any case, however, the posterior cingulum never connects with the metacone or the ridge between the metacone and hypocone. The result of the analysis of its variation is discussed in the next section.

Three roots are almost always present. The cross sections of these roots are oval in shape. The anterior root is the largest of the three, but the posterior one is the smallest. The fusion or division of the roots is very rarely observed (only three in thousands of specimens). In ASM 702675 from Layer 2 of Tanuki-ana Cave, the lingual root is fused with the anterior one, whereas the former is fused with the posterior one in one specimen from Layer 1 of Locality 3 of Ube Kosan Quarry (KUJC97208). In such cases, the total number of roots becomes two. On the other hand, the tip of the lingual root is divided into two in ASM 702114 from

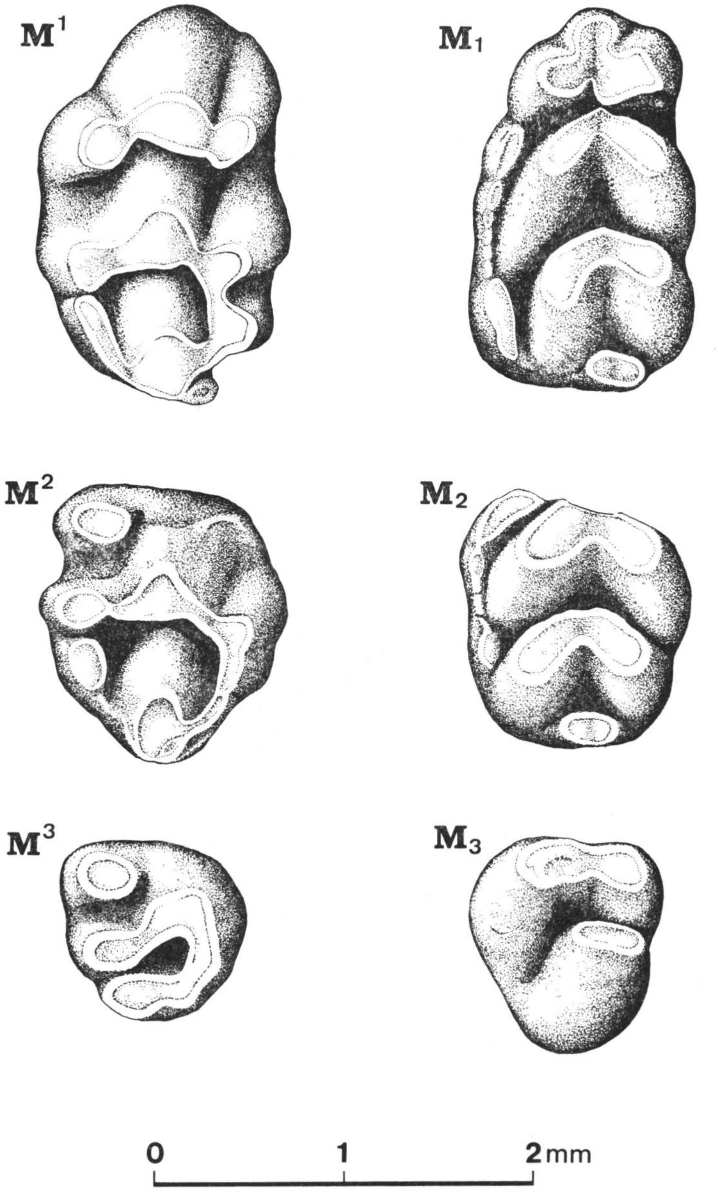


Fig. 173. *Apodemus speciosus*. Occlusal view of the left molars from Locality 3 of Ube Kosan Quarry. M^1, KUJC97198 from Layer 1; M^2, KUJC97428 from Layer 1; M^3, KUJC 97612 from Layer 17; M_1, KUJC97683 from Layer 3; M_2, KUJC 97813 from Layer 1; M_3, KUJC 97934 from Layer 1.

Layer 4 of Tanuki-ana Cave. In this case, the total number is apparently four.

M^2——

The crown is sub-round in occlusal view, and slightly broader than that of *A. argenteus*. It generally comprises two chevrons and one antero-lingual cusp (anterostyle). The anterior chevron is composed of the enterostyle, protocone and paracone, while the posterior chevron comprises the posterostyle, hypocone and metacone.

The anterostyle is round in occlusal view and somewhat elongated laterally. It is nearly as large as the enterostyle, and distinctly separated from the anterior chevron by a deep valley. The labial anterocone is poorly developed, but more or less variable in the degree of the development. It is sometimes completely absent, or sometimes represented by a weak and short cingulum on the antero-buccal face of the protocone. When it is recognizable as a cusp, it is generally very small and remarkably lower than the anterostyle. The variation of the labial anterocone is described in detail in the next section.

The disposition and shape of the cusps in the anterior and posterior chevrons are identical with those in the middle and posterior chevrons of M^1. The anterior and posterior chevrons of M^2 are easily connected to form a ring, because the enterostyle and paracone are arranged closely to the posterostyle and metacone respectively (the paracone-metacone connection is completed earlier as in M^1). The posterostyle is well-developed, but in general, it is slightly smaller than the metacone. The ridge between the metacone and hypocone is relatively long. The posterior cingulum is generally weak or absent as in M^1. If it is present, it never reaches the posterior face of the metacone in any stage of wear. The degree of the development of the posterior cingulum is analysed in the next section.

Three roots are always present (Table 87). The lingual root is remarkably larger than the other two roots. It usually shows an elliptical cross section elongated anteroposteriorly. In such a case, the central constriction is sometimes observed, which indicates the fusion of two roots. In some specimens, however, this root is much smaller and has a rounder section. The morphological variability of the lingual root is analysed in the next section.

The antero- and postero-buccal roots are round in cross section. The former is approximately as large as the latter.

M^3——

The crown is round or sub-triangular in occlusal view. It comprises two laminas and one antero-lingual cusp (anterostyle). The laminas are not chevron-shaped, but connect with each other on the buccal side.

The anterostyle is well developed and round in occlusal view. Lingual and labial anterocones are completely absent. The valley between the anterostyle and anterior lamina is deep and rather broad, but becomes somewhat shallower and narrower at its antero-buccal end. Consequently, the anterostyle sometimes connects with the protocone to form an additional transverse lamina along the anterior margin of the crown in worn teeth.

The true anterior lamina comprises the protocone and enterostyle. In slightly worn teeth, these cusps are clearly distinguishable from each other by a remarkable constriction of the lamina. Only in one living specimen of *A. speciosus* from Akiyoshi, this constriction becomes a deep valley which remains open even in considerably worn stages (the case of "abnormal type II" as described below; see Table 88), but such a pattern is not found in any fossil materials. Because the protocone is situated much anterior to the enterostyle, the anterior lamina is arranged obliquely to the transverse axis of the crown.

The posterior lamina comprises the paracone and hypocone. The paracone is closely set to the protocone, and almost fused with the latter so that these two cusps are almost indistinguishable in most specimens. The constriction between the paracone and hypocone is distinctly observed in slightly worn teeth. In some specimens, this constriction becomes a valley which is more distinct than that between the enterostyle and hypocone. In such a case, even when the latter valley disappears by wear, the former still remains (the case of "abnormal type I" as described below; see Table 88). A cusp is rarely recognizable between the paracone and hypocone. It possibly corresponds to the metacone. The posterior lamina extends along the posterior margin of the crown, and is approximately parallel to the anterior lamina.

The deep valley between the anterior and posterior laminas extends somewhat obliquely to the transverse axis of the crown, and usually opens lingually. It tapers between the enterostyle and hypocone to form an isthmus, but remarkably broadens buccally. When the occlusal surfaces of the enterostyle and hypocone are confluent by the wear of the crown, this broadened part becomes a round isolated pit.

Three roots are generally present; namely antero-lingual, antero-buccal and posterior roots. They are round in cross section. The antero-lingual and posterior roots have nearly the same size, and are slightly larger than the antero-buccal root. The posterior root remarkably extends postero-dorsally. The antero-lingual and antero-buccal roots are very rarely fused into one root which has an elliptical cross section elongated transversely. In such a case, the total number of roots becomes two.

Mandible——

The osteological characters of the mandible are well coincident with the above-mentioned generic characters. In comparison with the mandible of *A. argenteus*, that of the present fossils is decidedly larger and more heavily built. The diastema is relatively longer than that of *A. argenteus*. However the alveolar pattern with six pits is nearly identical with that of *A. argenteus* (Figs. 172, 180).

M_1——

The crown has a sub-rectangular outline in occlusal view, and comprises three chevrons. The anterior chevron is composed of three cusps, such as labial, medial and lingual anteroconids. The medial anteroconid is the smallest of the three. In slightly worn teeth, it is separated from the other two cusps, but soon connects with the medial part of the lingual anteroconid. As the wear is advanced, the

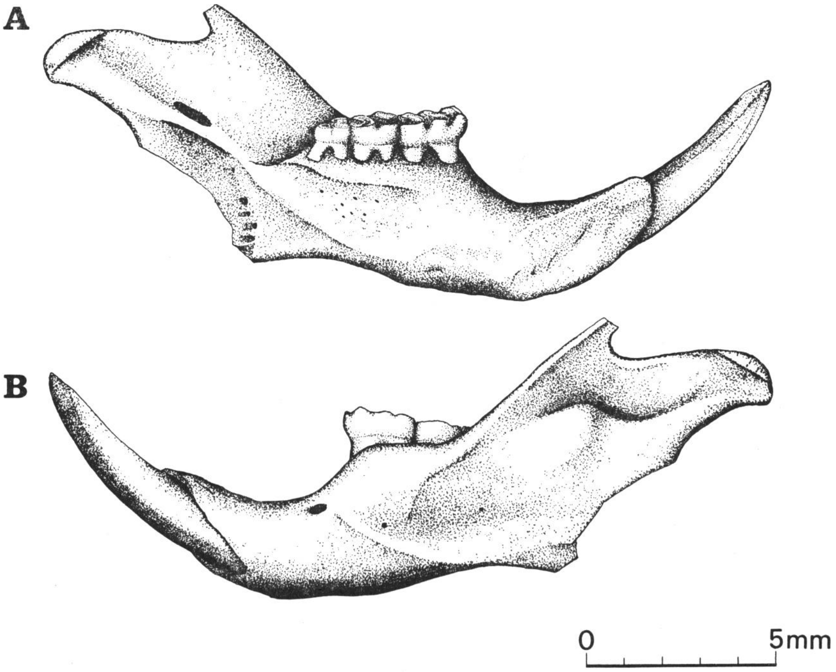


Fig. 174. *Apodemus speciosus*. Left mandible with I, M_1, M_2 and M_3 from Layer 1 of Locality 3 of Ube Kosan Quarry (KUJC97189). A, lingual view; B, buccal view.

occlusal surfaces of these three cusps are completely fused to form a "trifolium." The lingual anteroconid is somewhat anterior to the labial anteroconid in position. An indistinct posterior spur is sometimes observed at the medial part of the lingual anteroconid.

The middle chevron comprises the protoconid and metaconid which are united anteriorly. These cusps have nearly the same size, but are larger than the other cusps. The anterior mure is undeveloped. The valley between the anterior and middle chevrons is generally deep and distinct, but tapers at its medial part. Consequently, both chevrons connect with each other at this part in worn specimens. This connection is completed in the later stage of wear than that of the medial and lingual anteroconids. The buccal part of the valley extends postero-buccally along the buccal face of the protoconid and opens posteriorly. Otherwise, it sometimes opens buccally between the labial anteroconid and buccal accessory cusp (C3).

The posterior chevron comprises the hypoconid and entoconid which are also jointed anteriorly. The position of the former cusp is somewhat posterior to that of the latter. The medial mure is not observable. The valley between the middle and posterior chevrons is deep and broad, so that both chevrons are not confluent at their medial parts even in considerably worn teeth. The posterior cingulum is a distinct cusp between the hypoconid and entoconid. It is considerably lower than the posterior chevron and is slightly set lingually from the median line of the crown. Its occlusal surface is round or oval in shape.

Two to four accessory cusps are generally present on the buccal side of the crown. They usually form a continuous cusp row, but the degree of the development of each cusp is quite variable. The most posterior one (Cl) is the largest and situated on the buccal side of the hypoconid. It is remarkably lower than the hypoconid, and is oval in occlusal view. It is well separated from the hypoconid by a deep valley which joins anteriorly with the main valley between the middle and posterior chevrons. Therefore the occlusal surface of Cl is not connected with that of the hypoconid even in worn specimens. When the wear is much advanced, the juncture is first formed between the posterior ends of these cusps. A small accessory cusp corresponding to C2 is rarely observed on the anterior side of Cl.

A slender accessory cusp (C3) is always present on the buccal face of the protoconid. It is considerably lower than the protoconid. In some specimens, it becomes a distinct cusp which has an elliptical occlusal surface elongated antero-posteriorly. In other specimens, however, it is very slender like a wall. This accessory cusp is sometimes divided into two or three cuspules which are closely arranged in each other. Such a condition is well observed in slightly worn specimens. A low ridge usually extends from the anterior face of Cl to the posterior face of C3 through the position of C2. It forms an indistinct wall at the buccal entrance of the valley between the middle and posterior chevrons.

A small accessory cusp (C4) is sometimes present at the position anterior to C3. It is attached on the postero-buccal face of the labial anteroconid. If present, this cusp and C3 form a continuous wall at the buccal entrance of the valley between the anterior and middle chevrons.

The variation of these buccal accessory cusps is closely described in the next section.

Accessory cusps are very rarely observed on the lingual side of the crown. Only in two specimens, a small accessory cusp is found at the lingual entrance of the valley between the anterior and middle chevrons (KUJC100359 from Sugi-ana Cave and HUA-K00080 from the upper part of Horizon M of Kannondo Cave Site). On the other hand, a similar small cusp is present at the lingual entrance of the valley between the middle and posterior chevrons or on the lingual face of the entoconid only in four specimens (ASM 701656 from Locality 4 of Ube Kosan Quarry; HUA-K00240 from Horizon N and HUA-K00068 from the upper part of Horizon M of Kannondo Cave Site; ASM 702617 from Layers 3 to 2 of Tanuki-ana Cave).

M_1 always has two stout roots (anterior and posterior roots). However the small vestigial roots rarely found in M_1 of *A. argenteus* are not observed in any examined materials. The anterior root has an elliptical cross section which is elongated antero-posteriorly, but the axis of this ellipse is slightly oblique to the long axis of the tooth. The posterior root also has an elliptical cross section, but it is elongated transversely.

M_2——

The crown has a sub-quadrate occlusal outline with round corners. It comprises anterior and posterior chevrons and two isolated cusps (labial anteroconid and posterior cingulum). The width across the anterior chevron is nearly equal to or slightly larger than that across the posterior chevron.

The protoconid and metaconid are jointed anteriorly to form the anterior chevron. They are set approximately in the same transverse position. The protoconid is larger than the metaconid. The labial anteroconid is attached on the antero-buccal face of the protoconid, but is separated from the latter cusp by a narrow but distinct valley. It is considerably lower than the protoconid, and its occlusal surface is crescent-shaped. The lingual anteroconid and any accessory cusps are not observed on the anterior and lingual faces of the metaconid.

The posterior chevron is composed of the hypoconid and entoconid. These cusps have about the same size, but the former is slightly posterior relative to the latter. The posterior cingulum is well-developed and has a round or oval occlusal surface.

The buccal accessory cusps and/or cingulums are rather well-developed than those of *A. argenteus*. The number of the accessory cusps mostly ranges from 0 to 3. These cusps are generally small, but variable in the degree of the development. A cusp possibly corresponding to C2 is usually present at the buccal entrance of the valley between the anterior and posterior chevrons. In some specimens, this cusp is represented by a low ridge extending from the postero-buccal face of the protoconid to the buccal face of the hypoconid. Another accessory cusp (possibly Cl) is rarely observed on the buccal face of the hypoconid.

On the buccal face of the protoconid, an accessory cusp possibly corresponding to C3 is usually present immediately posterior to the labial anteroconid. It is sometimes confluent with the latter cusp, so that they are indistinguishable from each other in extreme cases. Another accessory cusp is rarely found between C3 and C2. In a few specimens, this cusp, C3 and C2 are united altogether to form a continuous ridge from the labial anteroconid to the buccal face of the hypoconid. The variation of these buccal accessory cusps is analysed in the next section.

M_2 always have two roots (anterior and posterior roots). The anterior root is smaller than the posterior root. These roots have elliptical or rectangular cross sections elongated transversely. Any vestigial rootlets are not observed between these two roots, as far as the present fossil materials are concerned.

M_3——

The crown has a sub-triangular outline with round corners in occlusal view, and comprises the anterior chevron and entoconid only. The transverse width across the anterior chevron is much larger than that across the entoconid.

The protoconid and metaconid are connected antero-medially at an obtuse angle to form the anterior chevron. The protoconid is somewhat larger than the metaconid, and slightly posterior to the latter cusp in position. The entoconid is the largest cusp and well separated from the anterior chevron by a deep transverse valley. It is columnar in three-dimensional shape, and somewhat tilts to the buccal side. Its occlusal surface is round or oval, but not so elongated as that of *A. argenteus*. In most specimens, it is slightly biassed lingually from the longitudinal midline of the crown.

Accessory cusps are usually absent from the anterior and both lateral sides of the crown. Exceptionally, a small vestigial accessory cusp is observed on the anterior face of the protoconid only in two specimens from Layers 1 and 3 of Locality 3 of Ube Kosan Quarry (KUJC97948 and 97980 respectively). It is considered to be the reduced labial anteroconid. Moreover another small accessory cusp is also very rarely found on the buccal face of the entoconid (observed in five specimens from Layers 1, 3, 17 and 18 of Locality 3 of Ube Kosan Quarry; KUJC97945, 97985, 98023, 98027 and 98033).

M_3 always has two roots, namely anterior and posterior roots. The former has an elliptical cross section elongated transversely, and extends straight ventrally. On the other hand, the latter extends postero-ventrally, and moreover slightly lingually. Its cross section is generally round in shape. The size of the posterior root is mostly larger than that of the anterior root.

Morphological analyses of the molars

Prestyle and precingulum of M^1——

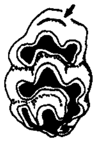
The frequencies of the appearances of the prestyle and precingulum on the anterior face of M^1 are analysed on the fossil materials of three different geological ages and on the recent *A. speciosus* (Table 82 and Fig. 175). Both prestyle and precingulum are absent in 83.1 to 97.1% of the total specimens, whereas both of them are present only in one specimen from Locality 3 of Ube Kosan Quarry (KUJC97388). The frequency of the specimens with the prestyle only ranges from 1.5 to 8.5%, while that with the precingulum only ranges from 1.5 to 9.1%. These facts indicate that the frequencies of the appearances of these structures are generally low in the examined populations. But, if compared with those in *A. argenteus*, they are remarkably higher (see Table 96 and Fig. 183). In regard to their temporal changes, the frequencies of the appearances of these structures gradually decrease from the Middle Pleistocene population to the recent one (Fig. 175).

Posterior spurs of the anterostyle and labial anterocone of M^1——

The frequencies of the appearances of the posterior spurs of the anterostyle and labial anterocone are analysed (Table 83 and Fig. 175). Both of the posterior spurs are absent in 48.9 to 78.4% of the total specimens, whereas both of them are present in 0 to 19.3% of the specimens. In 4.5 to 17.6% of the total specimens, the posterior spur is found only in the anterostyle. In 14.2 to 23.9% of the specimens, however, it is observed only in the labial anterocone. The frequencies of the appearances of these spurs are generally higher in the recent and Holocene populations than in the Late and Middle Pleistocene populations (Fig. 175). But as a whole, the frequencies are remarkably lower than those in *A. argenteus* (compare with Fig. 183).

Posterior cingulum of M^1——

Table 82. Morphological variation on the anterior face of M^1 of *Apodemus speciosus*. The absence or presence of the prestyle and/or precingulum is analysed. The number of the specimens belonging to each morphotype is tabulated. * total of all the layers.

	PRESTYLE(*ps*) AND PRECINGULUM (*prc*)				
LOCALITY	*ps* and *prc* absent 	*ps* present 	*prc* present 	*ps* and *prc* present 	TOTAL
RECENT MATERIALS					
Myogata	17	0	0	0	17
Gujohachiman	6	0	0	0	6
Ikeda	8	0	0	0	8
Mikawa Heights	26	0	1	0	27
Akiyoshi	9	1	0	0	10
HOLOCENE					
Tanuki-ana Cave					
Layer 1	6	0	0	0	6
Layer 2	35	2	0	0	37
Layers 2 to 3	16	0	0	0	16
Layer 3	20	3	2	0	25
Layer 4	79	10	3	0	92
Domen Site (Horizon V)	7	1	0	0	8
LATE PLEISTOCENE					
Kannondo Cave Site					
Horizon M (upper)	6	1	0	0	7
Horizon M (lower)	11	1	0	0	12
Horizon N	1	1	0	0	2
Horizon O (upper)	13	0	1	0	14
Horizon O (lower)	3	0	0	0	3
Horizon P	1	0	1	0	2
Sugi-ana Cave	12	1	0	0	13
MIDDLE PLEISTOCENE					
Loc.1 of Ube Kosan Quarry*	4	0	0	0	4
Loc.3 of Ube Kosan Quarry					
Layer 18	10	2	3	1	16
Layer 17	5	0	0	0	5
Layer 3	19	1	4	0	24
Layer 1	30	2	0	0	32
Loc.4 of Ube Kosan Quarry	13	1	0	0	14

In order to analyse its variability, three morphotypes are defined by the degree of the development of the posterior cingulum; namely "undeveloped type," "intermediate type" and "developed type" as figured in Table 84. The examined specimens are classified into these three types (Table 84). TOKUDA (1941b) proposed the similar morphotypes to analyse the variation of the recent forms such as "*A. ainu peninsulae*"

Table 83. Variation of the posterior spurs of the anterostyle and labial anterocone in M^1 of *Apodemus speciosus*. Four morphotypes are recognized by the presence or absence of these spurs. The number of the specimens belonging to each morphotype is tabulated. * total of all the layers.

LOCALITY	POSTERIOR SPURS OF ANTEROSTYLE (*as*) AND LABIAL ANTEROCONE (*la*)				TOTAL
	absent	present in *as*	present in *la*	present in *as* and *la*	
					
RECENT MATERIALS					
Myogata	7	2	6	2	17
Gujohachiman	2	0	1	2	5
Ikeda	6	0	1	1	8
Mikawa Heights	16	1	7	3	27
Akiyoshi	5	0	1	4	10
HOLOCENE					
Tanuki-ana Cave					
Layer 1	3	2	0	1	6
Layer 2	26	7	4	1	38
Layers 2 to 3	10	4	1	1	16
Layer 3	10	4	4	8	26
Layer 4	37	14	16	23	90
Domen Site (Horizon V)	6	2	0	0	8
LATE PLEISTOCENE					
Kannondo Cave Site					
Horizon M (upper)	4	0	1	0	5
Horizon M (lower)	9	1	1	0	11
Horizon N	1	0	1	0	2
Horizon O (upper)	11	1	2	0	14
Horizon O (lower)	3	0	0	0	3
Horizon P	1	0	1	0	2
Sugi-ana Cave	5	3	4	1	13
MIDDLE PLEISTOCENE					
Loc.1 of Ube Kosan Quarry*	1	1	2	0	4
Loc.3 of Ube Kosan Quarry					
Layer 18	9	1	6	0	16
Layer 17	4	1	0	0	5
Layer 3	20	1	2	1	24
Layer 1	19	1	9	3	32
Loc.4 of Ube Kosan Quarry	4	0	6	2	12

(=*A. peninsulae*), "*A. ainu ainu*" (=*A. speciosus ainu*) and several subspecies of *A. speciosus*. His type A corresponds to the undeveloped type of the present author. TOKUDA's types B and C also correspond to the intermediate type. TOKUDA's type D is identical

Table 84. Morphological variation of the posterior cingulum in M^1 of *Apodemus speciosus*. The specimens are classified into three morphotypes by the degree of the development of the posterior cingulum. The number of the specimens belonging to each morphotype is tabulated.
* total of all the layers.

LOCALITY	POSTERIOR CINGULUM			TOTAL
	Undeveloped	Intermediate	Developed	
				
RECENT MATERIALS				
Myogata	0	4	13	17
Gujohachiman	0	0	4	4
Ikeda	0	3	5	8
Mikawa Heights	2	7	16	25
Akiyoshi	0	2	8	10
HOLOCENE				
Tanuki-ana Cave				
Layer 1	0	1	3	4
Layer 2	0	21	15	36
Layers 2 to 3	0	8	5	13
Layer 3	3	12	10	25
Layer 4	3	35	49	87
Domen Site (Horizon V)	0	7	1	8
LATE PLEISTOCENE				
Kannondo Cave Site				
Horizon M (upper)	1	2	1	4
Horizon M (lower)	0	7	2	9
Horizon N	0	2	0	2
Horizon O (upper)	1	10	2	13
Horizon O (lower)	0	1	0	1
Horizon P	0	2	0	2
Sugi-ana Cave	1	9	3	13
MIDDLE PLEISTOCENE				
Loc.1 of Ube Kosan Quarry*	1	1	2	4
Loc.3 of Ube Kosan Quarry				
Layer 18	4	9	4	17
Layer 17	2	2	1	5
Layer 3	8	10	5	23
Layer 1	5	24	5	34
Loc.4 of Ube Kosan Quarry	1	6	7	14

with the developed type.

In the recent population, the frequency of the undeveloped type is only 3.1%, but those of the intermediate and developed types are 25.0 and 71.9% respectively (Fig. 175). Such a tendency is approximately coincident with the results of *A. speciosus*

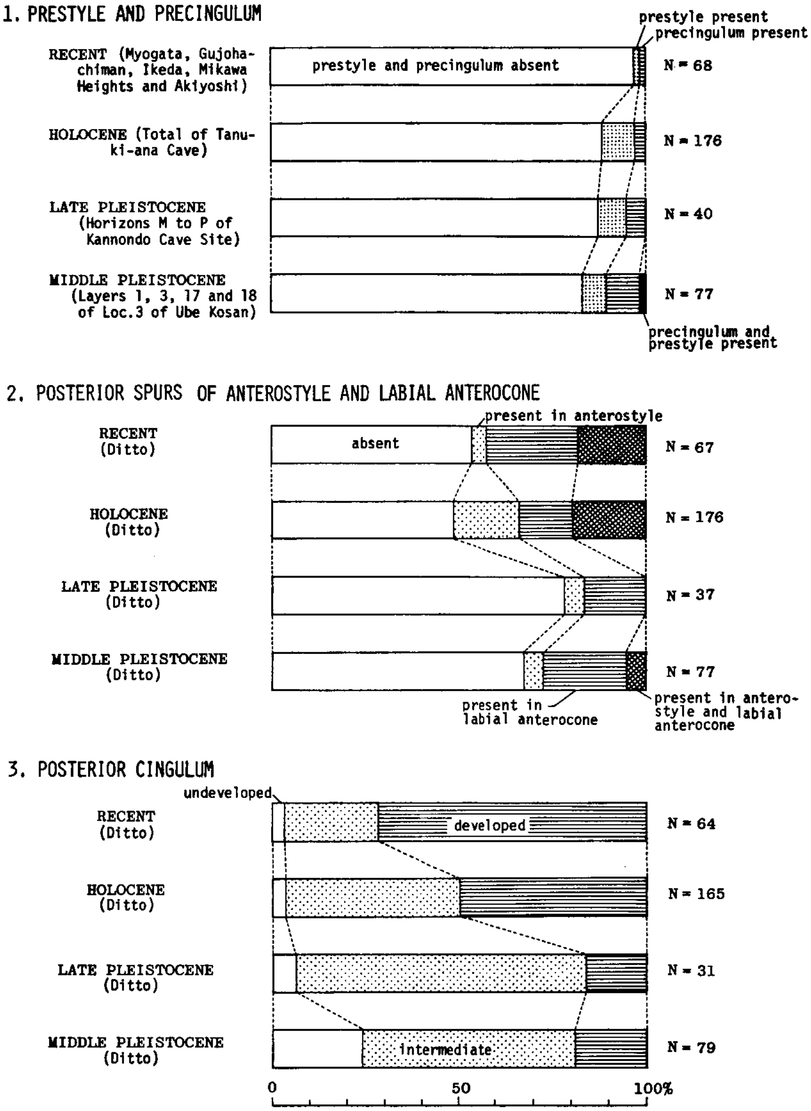


Fig. 175. Morphological variation in M^1 of *Apodemus speciosus*. The frequencies of each morphotype in the populations of various geological ages are illustrated. The data given in Tables 82, 83 and 84 are used. 1, variation of the prestyle and precingulum; 2, variation in the posterior spurs of the anterostyle and labial anterocone; 3, variation of the postrior cingulum. N, number of specimens.

analysed by TOKUDA (1941b). In the Holocene population, the frequency of the undeveloped type is still low (3.6%), but that of the intermediate type increases to be 46.7%. On the contrary, that of the developed type decreases to be 49.7%. Such frequencies are rather similar to those of "*A. ainu ainu*" provided by TOKUDA. In the Late Pleistocene population, the frequency of the undeveloped type somewhat increases to be 6.5%, but that of the developed type is remarkably diminished to be 16.1%. On the other hand, the intermediate type increases (77.4%). In the Middle Pleistocene population, the undeveloped type still increases to be 24.1%, whereas the intermediate and developed types appear in 57.0 and 19.0% of the total specimens respectively. The frequencies of each morphotype in the Late and Middle Pleistocene populations are quite different from those of "*A. ainu peninsulae*" analysed by TOKUDA (1941b), where the most specimens belong to the undeveloped type (ca. 95%).

Labial anterocone of M^2 ——

In order to analyse its variation, four morphotypes are defined by the degree of the development of the labial anterocone, as figured in Table 85. The numbers of the specimens belonging to each morphotype are given in the same table. The similar morphotypes described by TOKUDA (1941b) can be corresponded to the present ones. TOKUDA's types A and C are equivalent to the "well-developed" type of the present author. TOKUDA's type B corresponds to the "moderately developed" type. Although TOKUDA did not recognize the type of "labial anterocone represented as a cingulum," his type D possibly corresponds to this type and the "completely absent" type.

The frequency of the "completely absent" type fluctuates from 16.7 to 32.1%, while that of the type of "labial anterocone represented as a cingulum" is remarkably higher (41.1 to 66.7%). The "moderately developed" type appears in 12.5 to 36.8 % of the specimens, whereas the "well-developed" type are less frequently found (0 to 4.4%). The temporal changes of the frequency of each morphotype are not so obvious (Fig. 176).

Compared with the results of the analysis by TOKUDA (1941b), all the populations of the four different ages show the similar tendency in the frequency of each morphotype to that of *A. speciosus* by TOKUDA, but are somewhat different from his "*A. ainu ainu*." Moreover, they are decidedly different from his "*A. ainu peninsulae*," where the frequency of the "developed type" is remarkably higher (ca. 95%).

Posterior cingulum of M^2 ——

Three morphotypes are defined by the degree of the development of the posterior cingulum, as figured in Table 86. The examined specimens are classified into these three morphotypes in the same table. The similar morphotypes proposed by TOKUDA (1941b) can be corresponded to the present ones. TOKUDA's type A is equivalent to the undeveloped type of the present author. His types B and C correspond to the intermediate type. His type D also corresponds to the developed type. As far as TOKUDA's results are concerned, the frequencies of the undeveloped type, intermediate

Table 85. Morphological variation on the anterior face of M^2 of *Apodemus speciosus*. Four morphotypes are recognized by the degree of the development of the labial anterocone. The number of the specimens belonging to each morphotype is tabulated. * total of all the layers.

LOCALITY	LABIAL ANTEROCONE				TOTAL
	completely absent 	represented as a cingulum 	moderately developed 	well developed 	
RECENT MATERIALS					
Myogata	4	10	3	0	17
Gujohachiman	1	3	1	0	5
Ikeda	2	5	1	0	8
Mikawa Heights	12	10	6	1	29
Akiyoshi	3	1	4	2	10
HOLOCENE					
Tanuki-ana Cave					
Layer 1	2	2	1	0	5
Layer 2	1	12	7	0	20
Layers 2 to 3	6	2	4	0	12
Layer 3	2	5	3	1	11
Layer 4	8	18	20	1	47
Domen Site (Horizon V)	1	0	1	0	2
LATE PLEISTOCENE					
Kannondo Cave Site					
Horizon M (upper)	1	2	1	0	4
Horizon M (lower)	1	3	0	1	5
Horizon N	0	1	0	0	1
Horizon O (upper)	1	7	1	0	9
Horizon O (lower)	1	1	1	0	3
Horizon P	0	2	0	0	2
Sugi-ana Cave	0	4	1	0	5
MIDDLE PLEISTOCENE					
Loc.1 of Ube Kosan Quarry*	2	3	2	0	7
Loc.3 of Ube Kosan Quarry					
Layer 18	9	6	8	0	23
Layer 17	4	2	0	0	6
Layer 3	5	15	6	0	26
Layer 1	8	10	8	0	26
Loc.4 of Ube Kosan Quarry	3	4	3	0	10

type and developed type are 0, 15.7 and 84.3% in the recent *A. speciosus* respectively. However the analysis of the present author shows that they are 42.4, 11.9 and 45.8% respectively in the recent population of the same species (Fig. 176). The cause of such inconsistency can not be detected, because the revision of TOKUDA's materials is impossible. Therefore, the comparison with TOKUDA's results is not

Table 86. Morphological variation of the posterior cingulum in M^2 of *Apodemus speciosus*. The specimens are classified into three morphotypes by the degree of the development of the posterior cingulum. The number of the specimens belonging to each morphotype is tabulated.
* total of all the layers.

LOCALITY	POSTERIOR CINGULUM			TOTAL
	undeveloped 	intermediate 	developed 	
RECENT MATERIALS				
Myogata	10	2	5	17
Gujohachiman	1	0	2	3
Ikeda	4	0	2	6
Mikawa Heights	6	5	12	23
Akiyoshi	4	0	6	10
HOLOCENE				
Tanuki-ana Cave				
Layer 1	3	1	0	4
Layer 2	9	1	7	17
Layers 2 to 3	8	3	0	11
Layer 3	5	2	3	10
Layer 4	18	7	17	42
Domen Site (Horizon V)	0	1	1	2
LATE PLEISTOCENE				
Kannondo Cave Site				
Horizon M (upper)	2	0	2	4
Horizon M (lower)	1	2	1	4
Horizon N	1	0	0	1
Horizon O (upper)	6	1	0	7
Horizon O (lower)	2	0	0	2
Horizon P	2	0	0	2
Sugi-ana Cave	3	0	1	4
MIDDLE PLEISTOCENE				
Loc.1 of Ube Kosan Quarry*	4	1	2	7
Loc.3 of Ube Kosan Quarry				
Layer 18	11	3	1	15
Layer 17	5	0	1	6
Layer 3	15	8	1	24
Layer 1	20	5	1	26
Loc.4 of Ube Kosan Quarry	5	2	1	8

discussed here in regard to the variation of the posterior cingulum of M^2.

The results of the present analysis indicate that the undeveloped type gradually increases from the recent population (42.4%) to the Middle Pleistocene population (71.8%), while the developed type decreases from the former (45.7%) to the latter (5.6%). The tendency of these temporal changes is roughly coincident with that in the posterior cingulum of M^1 mentioned above.

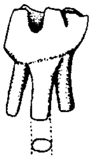
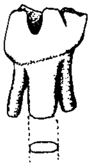
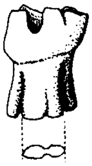
Morphology of the lingual root of M^2 ——

The following three morphotypes are recognized in order to analyse the morphological variability of the lingual root of M^2, as figured in Table 87:

1. The type of "oval in cross section": The lingual root is rather slender, and is oval in cross section.
2. The type of "elongated antero-posteriorly": The lingual root broadens antero-posteriorly so that its cross section shows a shape of elongated ellipse.
3. The type of "fusion of two roots": The lingual root is much elongated antero-posteriorly, and the constriction at its central part suggests the fusion of two roots.

The examined materials except the recent ones are classified into these three

Table 87. Morphological variation of the lingual root in M^2 of *Apodemus speciosus*. Three morphotypes are recognized as illustrated below. The number of the specimens belonging to each morphotype is tabulated.

LOCALITY	LINGUAL ROOT			TOTAL
	oval in cross section 	elongated antero-posteriorly 	fusion of two roots 	
HOLOCENE				
Tanuki-ana Cave				
Layer 1	1	2	1	4
Layer 2	5	11	0	16
Layers 2 to 3	2	3	0	5
Layer 3	1	3	0	4
Layer 4	12	9	1	22
Domen Site (Horizon V)	0	2	0	2
LATE PLEISTOCENE				
Kannondo Cave Site				
Horizon M (upper)	1	5	0	6
Horizon M (lower)	1	5	0	6
Horizon N	1	0	0	1
Horizon O (upper)	2	5	1	8
Horizon O (lower)	0	2	0	2
Horizon P	1	1	0	2
Sugi-ana Cave	3	1	0	4
MIDDLE PLEISTOCENE				
Loc.3 of Ube Kosan Quarry				
Layer 18	4	0	2	6
Layer 17	0	2	1	3
Layer 3	1	11	1	13
Layer 1	2	5	5	12

morphotypes (Table 87). The frequency of the type of "oval in cross section" is relatively high in the Holocene population (41.2%), but decreases towards the Middle Pleistocene population (20.6%). On the other hand, the type of "elongated anteroposteriorly" is most abundantly found in every population (52.9–72.0%). The

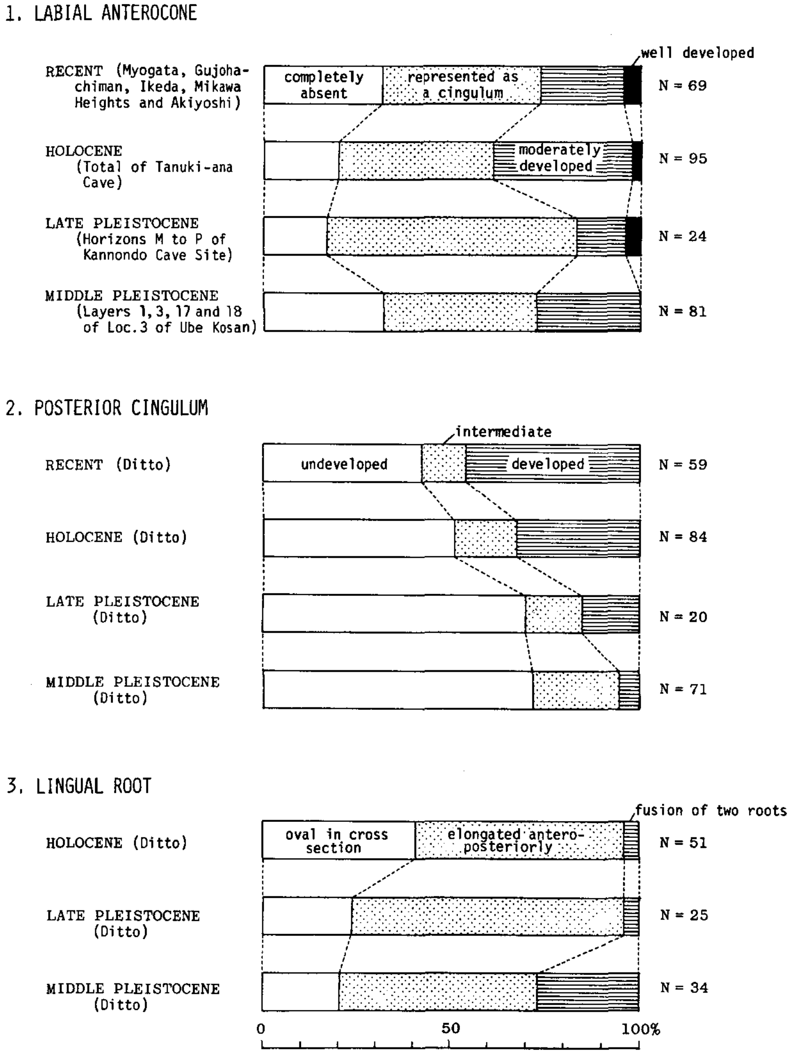


Fig. 176. Morphological variation in M^2 of *Apodemus speciosus*. The frequencies of each morphotype in the populations of various geological ages are illustrated. The data given in Tables 85, 86 and 87 are used. 1, variation of the labial anterocone; 2, variation of the posterior cingulum; 3, variation of the lingual root. N, number of specimens.

frequency of the type of "fusion of two roots" in the Holocene population (3.9%) is nearly the same as that in the Late Pleistocene population (4.0%), but the frequency is much higher in the Middle Pleistocene population (26.5%).

Occlusal pattern of M^3 ——

The following three morphotypes are defined by the opening direction of the valley between the anterior and posterior laminas (see Table 88):

1. Normal type: The valley opens postero-lingually.

Table 88. Variation in the occlusal pattern of M^3 of *Apodemus speciosus*. Three morphotypes are recognized as illustrated below. The number of the specimens belonging to each morphotype is tabulated. * total of all the layers.

LOCALITY	OCCLUSAL PATTERN OF M^3			TOTAL
	Normal type 	Abnormal type I 	Abnormal type II 	
RECENT MATERIALS				
Myogata	13	1	0	14
Gujohachiman	4	0	0	4
Ikeda	5	0	0	5
Mikawa Heights	15	1	0	16
Akiyoshi	7	1	1	9
HOLOCENE				
Tanuki-ana Cave				
Layer 1	2	0	0	2
Layer 2	3	0	0	3
Layers 2 to 3	3	0	0	3
Layer 3	1	0	0	1
Layer 4	9	1	0	10
LATE PLEISTOCENE				
Kannondo Cave Site				
Horizon M (upper)	2	0	0	2
Horizon M (lower)	1	0	0	1
Horizon O (upper)	4	0	0	4
Horizon O (lower)	3	0	0	3
Horizon P	0	1	0	1
Sugi-ana Cave	4	0	0	4
MIDDLE PLEISTOCENE				
Loc.1 of Ube Kosan Quarry*	3	1	0	4
Loc.3 of Ube Kosan Quarry				
Layer 18	6	3	0	9
Layer 17	1	1	0	2
Layer 3	12	0	0	12
Layer 1	11	2	0	13
Loc.4 of Ube Kosan Quarry	2	1	0	3

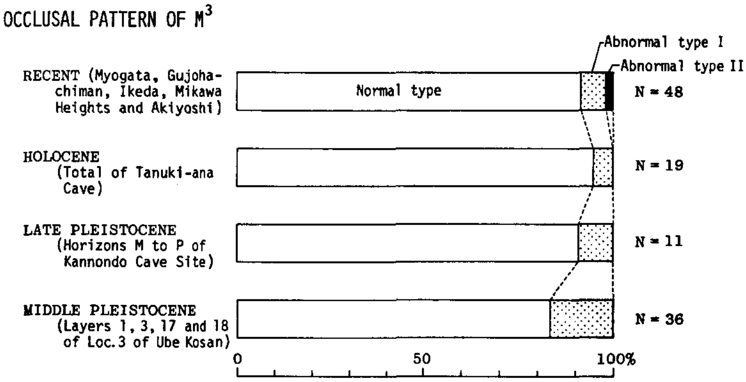


Fig. 177. Variation in the occlusal pattern of M^3 of *Apodemus speciosus*. The frequencies of each morphotype in the populations of various geological ages are illustrated. The data given in Table 88 are used. For detailed explanation of each morphotype, see text and Table 88. N, number of specimens.

2. Abnormal type I: The valley opens postero-buccally, so that the posterior lamina is interrupted.
3. Abnormal type II: The valley opens antero-lingually, so that the anterior lamina is interrupted.

The normal type is most abundantly found in every population (83.3–94.7%). The frequency of the abnormal type I gradually increases from the recent and Holocene populations (6.3 and 5.3% respectively) to the Middle Pleistocene population (16.7%). The abnormal type II is represented by only one recent specimen as already mentioned.

Buccal accessory cusps of M_1 ——

The variation of the buccal accessory cusps is analysed by recognizing the following six morphotypes (Fig. 178):

Morphotype A: C1 and C3 are present, but C3 is relatively small. This type is morphologically the simplest of the six.

Morphotype B: In addition to C1 and C3, C4 is existent on the postero-buccal face of the labial anteroconid. C3 is also small.

Morphotype C: C1 and C3 are present, but C3 is remarkably elongated antero-posteriorly. The morphology of C3 is quite variable. It is frequently divided into two cuspules, or it is sometimes slender like a ridge.

Morphotype D: This type is morphologically identical with the morphotype C except the additional presence of C4.

Morphotype E: This type is also identical with the morphotype C except the additional presence of C2.

Morphotype F: This type is the most complicate, because it is characterized by the presence of C1, C2, C4 and the elongated C3 (frequently divided into two cuspules).

The following three populations with different geological ages are examined:

1. Recent *A. speciosus* (N=56); combined materials from Myogata, Gujohachiman, Ikeda and Mikawa Heights.

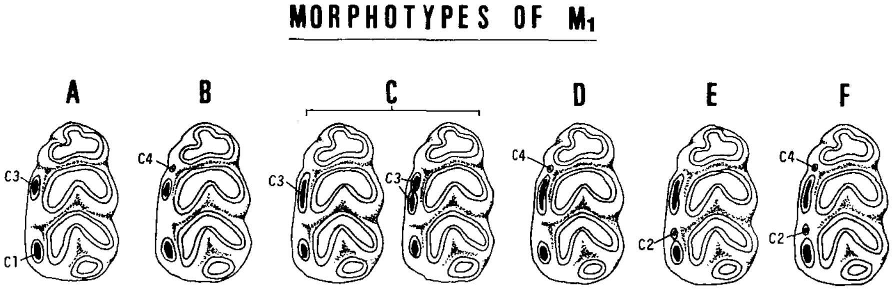


Fig. 178. Morphotypes of M_1 of *Apodemus*. Each morphotype is defined by the degree of the development of the buccal accessory cusps. For detailed explanation see text.

2. Late Pleistocene population (N=49); combined materials from Horizons M, N and O of Kannondo Cave Site.
3. Middle Pleistocene population (N=72); combined materials from Layers 1, 3, 17 and 18 of Locality 3 of Ube Kosan Quarry.

The morphotype C is most abundantly found in all the populations (43.8–55.1%). The frequency of the morphotype D fructuates from 18.8% (in the recent and Middle Pleistocene populations) to 32.7% (in the Late Pleistocene population). The morphotypes E and F are commonly found in the recent population (19.6 and 17.9% respectively), but become few in the Late Pleistocene population (6.1 and 4.1% respectively) and in the Middle Pleistocene population (4.2 and 4.2% respectively). On the other hand, the morphotype A is absent from the recent population, but gradually increases from the Late Pleistocene population (4.1%) to the Middle Pleistocene population (19.4%). The morphotype B is lacking in every population.

The temporal changes of the frequency of each morphotype are generally slight, although there seems to be the tendency that the frequencies of the simpler morphotypes increase but those of the more complicate ones decrease from the recent population to the Middle Pleistocene population. In comparison with *A. argenteus*, there are no significant differences in the frequency of each morphotype.

Buccal accessory cusps of M_2——

The variation of the buccal accessory cusps is analysed by recognizing the following eight morphotypes (Fig. 179):

Morphotype A: The buccal accessory cusps and cingulums are completely absent.

Morphotype B: A cingulum is present on the buccal entrance of the valley between the anterior and posterior chevrons.

Morphotype C: C3 is present immediately behind the labial anteroconid. Additionally, the cingulum as in the morphotype B is sometimes observed.

Morphotype D: C2 is present at the entrance of the valley between the anterior and posterior chevrons.

Morphotype E: Both C2 and C3 are present.

Morphotype F: In addition to C2 and C3, C1 is present.

Morphotype G: A strong continuous cingulum is present between the labial anteroconid and the buccal face of the hypoconid (the position of C2).

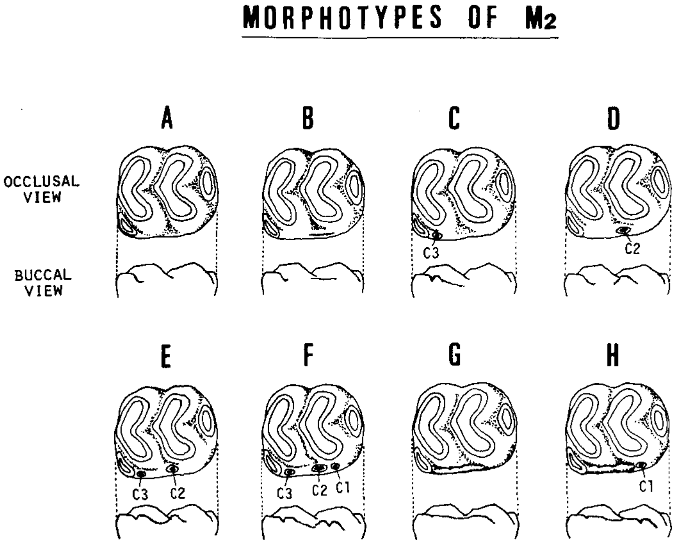


Fig. 179. Morphotypes of M_2 of *Apodemus*. Each morphotype is defined by the degree of the development of the buccal accessory cusps and cingulums. For detailed explanation see text.

Morphotype H: In addition to the cingulum as in the morphotype G, distinct C1 is present.

The following three populations with different geological ages are examined here:

1. Recent *A. speciosus* (N=58); combined materials from Myogata, Gujohachiman, Ikeda and Mikawa Heights.
2. Late Pleistocene population (N=26); combined materials from Horizons M, N and O of Kannondo Cave Site.
3. Middle Pleistocene population (N=61); combined materials from Layers 1, 3, 17 and 18 of Locality 3 of Ube Kosan Quarry.

The morphotype E is most abundant in every population (30.8–52.5%). The morphotypes G and D are commonly found; namely the frequencies of the former are 25.6% in the recent population, 23.1% in the Late Pleistocene population and 14.8% in the Middle Pleistocene population, and those of the latter are 15.5, 15.4 and 19.7% in the same order. The frequencies of the morphotypes C and B are somewhat fewer than those morphotypes; namely the frequencies of the former are 5.2, 11.5 and 3.3%, and those of the latter are 0, 11.5 and 4.9% in the above-mentioned order. On the other hand, the morphotypes A, F and H rarely occur. Their frequencies are generally less than 5%.

The significant temporal changes in the frequency of each morphotype are not observable from the results of the present analysis. But interspecifically, the frequencies in the examined populations are somewhat different from those in *A. argenteus*, where the simpler morphotypes (A, B and C) are more frequently found.

Measurements

The measurements of the representative mandibles are given in Table 89. Those of the molars are also given in Tables 90–95, and plotted in the scatter diagrams (Figs. 161–166). As concerns the molar sizes, some temporal changes are observable intraspecifically. However this problem will be discussed in a separate paper.

Comparisons

The osteological and dental characters of the present fossil materials are well coincident with those of the recent *A. speciosus* among the three species of the Japanese *Apodemus*. The fossil materials also bear slight differences in detailed dental morphology from the recent *A. speciosus* as already described, but these differences are too slight to deny the identification of the materials as *A. speciosus*. Therefore they are regarded as the intraspecific variations with geological ages. Because such comparisons are obviously insufficient to decide the accurate taxonomic position of the materials, more extensive comparisons with the living and fossil forms known from the Palaearctic Region are requested.

Comparisons with the East Asiatic living species of Apodemus ——

CORBET (1978) listed the following five species from East Asia outside Japan (He regarded *Apodemus giliacus* as a subspecies of *A. peninsulae*):

Apodemus agrarius (PALLAS, 1771)
Apodemus peninsulae (THOMAS, 1906)
Apodemus draco (BARRETT-HAMILTON, 1900)
Apodemus latronum THOMAS, 1911
Apodemus semotus THOMAS, 1908

CORBET noted "*A. semotus* is close to *A. draco* and could be conspecific with it." On the other hand, XIA (1984) recently considered *A. chevrieri* (MILNE-EDWARDS, 1868) as a full species which is regarded as a subspecies of *A. agrarius* by many authors.

The present fossil materials are easily distinguishable from *A. agrarius* in the numbers of the roots of the upper molars and the detailed morphology of their crowns. In *A. agrarius*, M^1, M^2 and M^3 have four, four and two (or three) roots respectively, while all of them are three-rooted in the present fossils. The posterior cingulums of M^1 and M^2 are absent or weak in *A. agrarius*, but they are relatively well-developed in the present fossils. The complete absence of the labial anterocone from M^2 is characteristic to *A. agrarius*, whereas this cusp is sometimes present in the present fossils. The differences in the occlusal pattern of M^3 are also observable between them.

A. peninsulae (excluding "*giliacus*" from CORBET's definition) is generally similar to *A. giliacus*. As already described, the present fossils can be discriminated from *A. giliacus* by the detailed dental morphology and size. In comparison with *A. peninsulae*, the same differences are also observed. Namely, in *A. peninsulae*, the size is somewhat smaller and the labial anterocone of M^2 is more conspicuous. The posterior cingulums of M^1 and M^2 of *A. peninsulae* are mostly of "*giliacus*" type, and

Table 89. Measurements of the mandibles of *Apodemus speciosus* in mm. The numbers on the left side correspond to those in Fig. 72.

	Kannondo Cave Site Horizon I (Holocene)			Kumai-shi-do Cave, F_4	Kannondo Site Horizon M (Late Pleistocene)		Sugi-ana Cave		Locality 3 of Ube Kosan Quarry					
									Layer 17	Layer 4	Layer 3			Layer 1
	HUA-K 03948	HUA-K 03949	HUA-K 03950	YKS 00419	HUA-K 00021	HUA-K 00025	KUJC 100300	KUJC 100301	KUJC 97351	KUJC 98058	KUJC 97268	KUJC 97269	KUJC 97273	KUJC 97189
1. Total length of the mandible (id to goc)	14.54	–	–	–	–	–	–	–	–	–	–	–	–	–
2. Ditto (id to the condyle)	–	17.41	–	–	–	–	–	–	–	–	–	–	–	–
3. Length from the tip of the incisor to the condyle	–	19.10	–	–	–	–	–	–	–	–	–	–	19.30	–
4. Length of the horizontal ramus	9.34	10.11	9.40	–	9.70	–	–	–	9.39	8.62	–	–	–	–
5. Length of the diastema	5.05	5.65	5.17	–	5.09	–	–	–	5.31	4.70	–	–	–	–
6. Length of the ascending ramus (the posterior border of M_3 to the condyle)	–	7.47	–	–	–	–	7.58	–	–	–	–	–	7.84	–
7. Ditto (the posterior border of M_3 to goc)	5.77	–	–	–	–	–	–	–	–	–	–	–	–	–
8. Height of the ascending ramus (gov to the highest point of the condyle)	6.53	–	–	–	–	–	–	–	–	–	–	–	7.24	–
10. Ditto (gov to the mandibular incision)	6.13	–	–	–	–	–	–	–	–	–	–	–	6.58	–
12. Height of the horizontal ramus at M_1	3.05	3.31	3.06	3.43	–	–	3.38	3.71	3.49	3.08	3.42	3.74	3.40	3.34
13. Height of the horizontal ramus at M_3	2.65	2.93	2.65	2.53	2.71	–	2.77	3.28	2.84	2.45	2.83	2.95	2.92	2.73
14. Maximum thickness of the horizontal ramus	1.90	2.04	1.84	–	–	1.65	2.19	2.06	2.08	1.97	1.85	2.24	2.14	1.91
15. Length of the molar row (M_1 to M_3) at the crowns	4.58	4.55	4.39	–	–	4.37	4.20	4.52	–	–	–	4.31	–	4.04
16. Ditto at the alveoli	4.44	4.58	4.33	4.33	4.68	4.35	4.22	4.46	4.23	4.09	4.19	4.38	4.36±	4.09
17. Length of the molar row (M_1 to M_2) at the crowns	3.42	3.45	3.25	–	–	3.26	3.11	3.32	3.10	–	–	3.27	–	3.08
18. Ditto at the alveoli	3.15	3.19	3.04	2.97	3.36	3.04	2.99	2.90	2.85	2.85	2.93	3.07	3.10±	2.90

Table 90. Measurements of M¹ of *Apodemus speciosus*. * MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	3	2.21	2.27	2.35	–	3	1.41	1.44	1.48	–
Nopporo	2	1.89	1.97	2.04	–	2	1.38	1.40	1.41	–
Otaki	2	2.20	2.23	2.25	–	2	1.41	1.44	1.47	–
HONSHU										
Sugaya	1	–	2.13	–	–	1	–	1.32	–	–
Nikko	2	1.95	2.07	2.20	–	2	1.28	1.35	1.42	–
Nojiri-ko	3	1.97	2.04	2.14	–	3	1.28	1.32	1.35	–
Myogata	19	1.93	2.10	2.30	0.09	19	1.24	1.35	1.44	0.05
Gujohachiman	7	2.00	2.09	2.24	0.08	7	1.24	1.34	1.40	0.05
Ikeda	8	1.92	2.06	2.19	0.10	8	1.23	1.32	1.39	0.05
Mikawa Heights	28	1.99	2.12	2.28	0.08	28	1.27	1.35	1.43	0.04
Mineyama	3	2.06	2.17	2.23	–	3	1.28	1.30	1.32	–
Taishaku	1	–	2.16	–	–	1	–	1.44	–	–
Akiyoshi	10	1.89	2.16	2.24	0.09	10	1.28	1.35	1.43	0.05
HOLOCENE										
Husen-ana Cave	21	2.04	2.19	2.32	0.08	21	1.27	1.38	1.44	0.04
Tanuki-ana Cave (Layer 2)	5	1.92	2.10	2.25	0.13	5	1.26	1.34	1.40	0.05
Domen Site (Horizon V)	8	2.06	2.13	2.22	0.05	9	1.29	1.35	1.38	0.03
Kannondo Cave Site										
Horizon unknown	2	2.02	2.10	2.18	–	2	1.35	1.36	1.37	–
Horizon I	5	2.15	2.20	2.25	0.04	5	1.37	1.41	1.44	0.03
Horizon J	1	–	2.29	–	–	1	–	1.44	–	–
Horizon K	1	–	2.23	–	–	1	–	1.43	–	–
Suse Quarry (West Fissure)*	2	2.08	2.09	2.10	–	2	1.35	1.36	1.36	–
LATE PLEISTOCENE										
Kumaishi-do Cave										
F_1, F_2 and F_4	13	1.99	2.15	2.30	0.09	13	1.25	1.33	1.43	0.06
F_3	60	1.92	2.13	2.35	0.09	60	1.19	1.34	1.45	0.05
Kannondo Cave Site										
Horizon M (upper)	6	2.06	2.14	2.22	0.06	7	1.27	1.35	1.40	0.04
Horizon M (lower)	10	2.10	2.17	2.29	0.05	11	1.29	1.35	1.42	0.04
Horizon N	2	2.13	2.17	2.21	–	2	1.29	1.35	1.40	–
Horizon O (upper)	6	2.04	2.12	2.29	0.08	6	1.31	1.36	1.45	0.04
Horizon O (lower)	2	2.01	2.07	2.14	–	3	1.34	1.35	1.36	–
Horizon P	2	1.91	2.04	2.16	–	2	1.22	1.30	1.38	–
Yage Quarry										
Site 4	1	–	2.15	–	–	1	–	1.32	–	–
Site 5	2	2.15	2.17	2.19	–	2	1.33	1.34	1.35	–
Sugi-ana Cave	13	2.02	2.16	2.25	0.06	13	1.29	1.35	1.40	0.03
Loc.2 of Ube Kosan Quarry	–	–	–	–	–	1	–	1.36	–	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 1	1	–	2.06	–	–	1	–	1.28	–	–
Layer 2	2	2.01	2.09	2.17	–	2	1.24	1.27	1.31	–
Layer 3	1	–	2.32	–	–	1	–	1.40	–	–
Loc.3 of Ube Kosan Quarry										
Layer 18	16	1.98	2.18	2.35	0.11	16	1.24	1.34	1.46	0.06
Layer 17	5	1.94	2.18	2.33	0.15	5	1.25	1.36	1.42	0.06
Layer 3	24	1.96	2.16	2.38	0.10	25	1.23	1.33	1.43	0.06
Layer 1	33	1.89	2.15	2.28	0.08	34	1.23	1.33	1.45	0.05
Loc.4 of Ube Kosan Quarry	9	2.07	2.16	2.27	0.07	11	1.23	1.31	1.40	0.04

its incisive foramina open more anteriorly.

The available information on the osteological and dental characters of *A. draco* and *A. latronum* is rather scarce. Although M¹ of *A. draco* has three roots as the present fossils, the general size of this species is decidedly smaller. On the other hand, *A. latronum* has about the same size as the present fossils, but the lingual root of its M¹ is rather broader and sometimes divided into two or three parts.

Table 91. Measurements of M^2 of *Apodemus speciosus*. * MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	3	1.48	1.52	1.55	–	3	1.33	1.39	1.43	–
Nopporo	1	–	1.50	–	–	1	–	1.29	–	–
Otaki	2	1.41	1.46	1.52	–	2	1.34	1.37	1.39	–
HONSHU										
Sugaya	1	–	1.35	–	–	1	–	1.26	–	–
Nikko	2	1.29	1.42	1.55	–	2	1.26	1.34	1.42	–
Nojiri-ko	2	1.30	1.34	1.38	–	2	1.28	1.30	1.32	–
Myogata	19	1.28	1.42	1.52	0.06	19	1.24	1.31	1.39	0.04
Gujohachiman	7	1.16	1.32	1.46	0.10	7	1.20	1.30	1.40	0.07
Ikeda	8	1.29	1.37	1.44	0.05	8	1.16	1.26	1.32	0.05
Mikawa Heights	30	1.29	1.41	1.50	0.06	30	1.23	1.31	1.39	0.04
Mineyama	3	1.30	1.43	1.54	–	3	1.25	1.28	1.30	–
Taishaku	1	–	1.34	–	–	1	–	1.39	–	–
Akiyoshi	10	1.32	1.40	1.52	0.07	10	1.24	1.32	1.40	0.06
HOLOCENE										
Husen-ana Cave	6	1.37	1.47	1.55	0.07	6	1.29	1.33	1.39	0.04
Tanuki-ana Cave (Layer 2)	5	1.20	1.33	1.46	0.09	5	1.26	1.31	1.36	0.04
Domen Site (Horizon V)	2	1.44	1.45	1.46	–	2	1.30	1.32	1.33	–
Kannondo Cave Site										
Horizon unknown	1	–	1.50	–	–	1	–	1.32	–	–
Horizon I	8	1.40	1.45	1.53	0.04	8	1.31	1.36	1.38	0.02
Horizon J	2	1.42	1.46	1.50	–	2	1.31	1.34	1.37	–
Horizon K	1	–	1.43	–	–	1	–	1.34	–	–
Suse Quarry (West Fissure)*	3	1.22	1.39	1.48	–	3	1.26	1.28	1.31	–
LATE PLEISTOCENE										
Kumaishi-do Cave										
F_1, F_2 and F_4	3	1.37	1.40	1.43	–	3	1.24	1.25	1.26	–
F_3	25	1.29	1.39	1.57	0.07	25	1.21	1.29	1.38	0.04
Kannondo Cave Site										
Horizon M (upper)	5	1.38	1.46	1.56	0.06	5	1.27	1.32	1.36	0.03
Horizon M (lower)	6	1.33	1.41	1.50	0.06	6	1.26	1.32	1.39	0.04
Horizon N	1	–	1.49	–	–	1	–	1.36	–	–
Horizon O (upper)	3	1.41	1.45	1.51	–	3	1.23	1.28	1.36	–
Horizon O (lower)	2	1.41	1.44	1.47	–	2	1.24	1.26	1.29	–
Horizon P	2	1.29	1.34	1.39	–	2	1.18	1.20	1.21	–
Yage Quarry (Site 4)*	1	–	1.25	–	–	1	–	1.24	–	–
Sugi-ana Cave	4	1.31	1.39	1.47	–	5	1.28	1.33	1.38	0.04
Aisawa Quarry	1	–	1.35	–	–	1	–	1.30	–	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	2	1.57	1.58	1.58	–	2	1.31	1.35	1.40	–
Layer 3	4	1.48	1.53	1.56	–	4	1.24	1.31	1.39	–
Layer 4	1	–	1.49	–	–	1	–	1.32	–	–
Loc.3 of Ube Kosan Quarry										
Layer 18	21	1.38	1.49	1.59	0.06	22	1.19	1.29	1.35	0.05
Layer 17	6	1.35	1.47	1.57	0.07	6	1.27	1.29	1.32	0.02
Layer 3	26	1.22	1.44	1.58	0.08	23	1.17	1.28	1.38	0.05
Layer 1	25	1.22	1.43	1.55	0.09	25	1.19	1.28	1.40	0.05
Loc.4 of Ube Kosan Quarry	9	1.35	1.42	1.46	0.04	9	1.22	1.27	1.35	0.04

A. semotus is slightly smaller than the present fossils. As TOKUDA (1941b) described, in *A. semotus*, the buccal accessory cusps and cingulums of M$_1$ and M$_2$ are best developed among the Far Eastern species of *Apodemus*. Therefore they seem to be more remarkable than those of the present fossils.

Comparisons with other living species of Apodemus ——

Other than the above-mentioned species, the following are known from the Palae-

Table 92. Measurements of M^3 of *Apodemus speciosus*. * MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	3	0.93	1.01	1.07	–	3	0.95	1.02	1.05	–
Nopporo	1	–	1.02	–	–	1	–	0.98	–	–
Otaki	2	0.87	0.90	0.93	–	2	0.85	0.90	0.94	–
HONSHU										
Sugaya	1	–	0.95	–	–	1	–	0.91	–	–
Nikko	2	0.91	0.97	1.03	–	2	0.94	1.01	1.08	–
Nojiri-ko	2	0.96	0.98	1.00	–	2	0.90	0.91	0.92	–
Myogata	18	0.92	0.98	1.05	0.04	18	0.85	0.96	1.04	0.05
Gujohachiman	7	0.87	0.92	0.97	0.04	7	0.89	0.95	1.07	0.06
Ikeda	8	0.85	0.95	1.03	0.06	8	0.82	0.93	1.01	0.05
Mikawa Heights	26	0.86	0.97	1.04	0.04	26	0.86	0.96	1.04	0.04
Mineyama	3	0.92	0.99	1.03	–	3	0.84	0.91	0.95	–
Taishaku	1	–	1.02	–	–	1	–	1.05	–	–
Akiyoshi	10	0.90	0.94	1.04	0.04	10	0.87	0.96	1.09	0.06
HOLOCENE										
Husen-ana Cave	2	0.93	0.96	0.98	–	2	0.99	1.01	1.02	–
Kannondo Cave Site										
Horizon unknown	1	–	0.98	–	–	1	–	0.98	–	–
Horizon I	7	0.93	1.02	1.12	0.06	7	0.94	0.98	1.03	0.03
Horizon J	2	1.00	1.01	1.02	–	2	0.94	0.98	1.02	–
Horizon K	1	–	0.90	–	–	1	–	0.92	–	–
Suse Quarry (West Fissure)*	4	0.95	0.97	1.01	–	4	0.93	0.95	0.96	–
LATE PLEISTOCENE										
Kumaishi-do Cave										
F_1, F_2 and F_4	2	0.95	0.98	1.01	–	2	0.84	0.91	0.98	–
F_3	18	0.84	0.94	1.01	0.05	18	0.84	0.93	1.08	0.06
Kannondo Cave Site										
Horizon M (upper)	2	1.02	1.04	1.07	–	2	0.98	0.99	1.00	–
Horizon M (lower)	1	–	0.99	–	–	2	0.97	0.98	1.00	–
Horizon O (lower)	4	0.98	1.01	1.04	–	4	0.90	0.93	0.96	–
Horizon P	1	–	0.91	–	–	1	–	0.95	–	–
Sugi-ana Cave	4	0.95	0.98	1.06	–	4	0.92	0.96	1.02	–
Loc.2 of Ube Kosan Quarry	1	–	0.96	–	–	1	–	0.94	–	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	3	0.87	0.92	0.95	–	3	0.95	0.98	1.04	–
Layer 3	1	–	1.00	–	–	1	–	0.99	–	–
Loc.3 of Ube Kosan Quarry										
Layer 18	13	0.83	0.93	0.99	0.05	13	0.89	0.95	1.03	0.04
Layer 17	2	0.91	0.94	0.96	–	2	0.96	0.96	0.97	–
Layer 3	19	0.87	0.95	1.06	0.05	20	0.84	0.94	1.06	0.06
Layer 1	21	0.85	0.96	1.05	0.06	21	0.86	0.95	1.05	0.06
Loc.4 of Ube Kosan Quarry	4	0.88	0.92	0.98	–	6	0.84	0.95	1.08	0.07

arctic Region as representative species:

Apodemus mystacinus (DANFORD et ALSTON, 1877)
Apodemus flavicollis (MELCHIOR, 1834)
Apodemus sylvaticus (LINNAEUS, 1758)
Apodemus microps KRATOCHVIL et ROSICKY, 1952

M^1 and M^2 of these species almost always have four roots respectively (ZIMMERMANN, 1962). Therefore they are readily distinguishable from the present fossils.

Comparisons with the Chinese fossil Apodemus——

As already stated, "*A.* cf. *sylvaticus*" from Huaiyu is the only representative of the

Table 93. Measurements of M_1 of *Apodemus speciosus*. ° Grids B–0 and B–1, * MATSUHASHI Collection, ** partly MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	3	1.89	1.99	2.05	–	3	1.19	1.25	1.31	–
Nopporo	2	1.79	1.85	1.90	–	2	1.18	1.19	1.21	–
Otaki	2	2.03	2.04	2.05	–	2	1.25	1.26	1.27	–
HONSHU										
Sugaya	1	–	1.92	–	–	1	–	1.19	–	–
Nikko	2	1.92	1.94	1.97	–	2	1.20	1.20	1.21	–
Nojiri-ko	3	1.89	1.91	1.93	–	3	1.10	1.17	1.24	–
Myogata	19	1.78	1.92	2.04	0.06	19	1.12	1.19	1.26	0.04
Gujohachiman	7	1.83	1.93	2.05	0.10	7	1.10	1.19	1.24	0.05
Ikeda	8	1.80	1.90	2.10	0.10	8	1.08	1.16	1.24	0.06
Mikawa Heights	31	1.85	1.95	2.09	0.07	31	1.12	1.19	1.25	0.04
Mineyama	3	1.86	1.89	1.93	–	3	1.11	1.14	1.18	–
Taishaku	1	–	1.91	–	–	1	–	1.18	–	–
Akiyoshi	10	1.82	1.92	2.00	0.06	10	1.14	1.19	1.24	0.03
HOLOCENE										
Anagami Site										
Layer 4°	1	–	1.95	–	–	1	–	1.15	–	–
Layer 6°	1	–	1.95	–	–	1	–	1.17	–	–
Husen-ana Cave	17	1.84	1.99	2.13	0.07	17	1.16	1.21	1.30	0.04
Tanuki-ana Cave (Layer 2)	4	1.89	1.95	2.04	–	4	1.20	1.22	1.24	–
Domen Cave Site										
Horizon unknown	3	1.96	2.06	2.16	–	3	1.18	1.21	1.25	–
Horizon V	4	1.97	2.00	2.06	–	5	1.18	1.20	1.24	0.02
Kannondo Cave Site										
Horizon unknown	11	1.84	1.97	2.05	0.07	11	1.12	1.21	1.25	0.04
Horizon F	1	–	1.96	–	–	1	–	1.23	–	–
Horizon H	3	1.93	1.99	2.04	–	3	1.19	1.23	1.27	–
Horizon I	31	1.89	2.00	2.17	0.07	33	1.16	1.24	1.32	0.04
Horizon J	24	1.82	1.99	2.14	0.09	24	1.12	1.23	1.32	0.05
Horizon K	15	1.85	1.99	2.16	0.08	15	1.04	1.20	1.26	0.06
Horizon L	14	1.77	1.96	2.09	0.09	14	1.12	1.20	1.25	0.04
Suse Quarry (West Fissure)*	20	1.80	1.97	2.08	0.07	20	1.12	1.19	1.28	0.04
LATE PLEISTOCENE										
Suse Quarry (East Fissure)*	7	1.79	1.91	2.01	0.06	7	1.10	1.16	1.21	0.04
Kumaishi-do Cave										
F_1, F_2 and F_4	18	1.86	1.96	2.07	0.06	18	1.07	1.17	1.28	0.05
F_3	65	1.80	1.93	2.08	0.07	65	1.09	1.15	1.24	0.04
Kannondo Cave Site										
Horizon M (upper)	22	1.79	1.96	2.13	0.08	22	1.09	1.17	1.27	0.04
Horizon M (lower)	23	1.81	1.95	2.10	0.07	25	1.10	1.19	1.25	0.05
Horizon N	18	1.82	1.99	2.16	0.08	18	1.08	1.19	1.36	0.06
Horizon O (upper)	4	1.83	1.93	2.08	–	4	1.10	1.16	1.20	–
Horizon O (lower)	5	1.89	1.99	2.17	0.10	5	1.14	1.17	1.24	0.04
Horizon P	5	1.84	1.93	1.98	0.05	6	1.11	1.16	1.21	0.03
Yage Quarry**										
Site 2	–	–	–	–	–	1	–	1.19	–	–
Site 4	4	1.80	1.92	2.03	–	4	1.15	1.17	1.18	–
Sugi-ana Cave	11	1.86	1.94	2.01	0.05	10	1.13	1.20	1.26	0.04
Aisawa Quarry	2	2.06	2.07	2.08	–	2	1.22	1.24	1.25	–
Loc.2 of Ube Kosan Quarry	1	–	1.88	–	–	1	–	1.13	–	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 1	3	1.87	1.94	2.01	–	3	1.14	1.15	1.17	–
Layer 2	3	1.86	1.94	2.03	–	3	1.10	1.12	1.16	–
Layer 3	2	1.94	1.94	1.95	–	2	1.12	1.16	1.19	–
Loc.3 of Ube Kosan Quarry										
Layer 18	22	1.75	1.94	2.03	0.06	22	1.12	1.17	1.25	0.04
Layer 17	7	1.87	1.95	2.04	0.07	7	1.08	1.16	1.25	0.05
Layer 3	24	1.78	1.94	2.07	0.09	29	1.05	1.16	1.28	0.06
Layer 1	21	1.76	1.91	1.99	0.06	20	1.08	1.14	1.19	0.03
Loc.4 of Ube Kosan Quarry	6	1.72	1.87	1.94	0.08	10	1.07	1.15	1.27	0.06

Table 94. Measurements of M_2 of *Apodemus speciosus*. ° Brids B-0 and B-1, * MATSUHASHI Collection, ** partly MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	3	1.43	1.47	1.52	–	3	1.26	1.32	1.38	–
Nopporo	2	1.41	1.43	1.46	–	2	1.23	1.26	1.29	–
Otaki	2	1.41	1.44	1.47	–	2	1.27	1.27	1.28	–
HONSHU										
Sugaya	1	–	1.35	–	–	1	–	1.21	–	–
Nikko	2	1.34	1.40	1.46	–	2	1.17	1.21	1.25	–
Nojiri-ko	2	1.44	1.44	1.45	–	2	1.18	1.20	1.22	–
Myogata	19	1.27	1.41	1.52	0.06	19	1.16	1.22	1.29	0.04
Gujohachiman	7	1.30	1.36	1.44	0.06	7	1.12	1.21	1.26	0.05
Ikeda	8	1.34	1.37	1.41	0.02	8	1.13	1.18	1.24	0.03
Mikawa Heights	31	1.31	1.40	1.51	0.06	31	1.14	1.20	1.30	0.04
Mineyama	3	1.41	1.44	1.49	–	3	1.18	1.20	1.22	–
Taishaku	1	–	1.42	–	–	1	–	1.23	–	–
Akiyoshi	10	1.25	1.41	1.47	0.06	10	1.16	1.23	1.32	0.05
HOLOCENE										
Anagami Site										
Layer 4°	1	–	1.42	–	–	1	–	1.21	–	–
Layer 6°	1	–	1.34	–	–	1	–	1.18	–	–
Husen-ana Cave	8	1.31	1.41	1.49	0.06	8	1.17	1.25	1.36	0.06
Tanuki-ana Cave (Layer 2)	9	1.32	1.41	1.50	0.06	9	1.12	1.21	1.30	0.06
Domen Cave Site										
Horizon unknown	1	–	1.36	–	–	1	–	1.28	–	–
Horizon V	7	1.31	1.36	1.45	0.05	8	1.19	1.23	1.27	0.03
Kannondo Cave Site										
Horizon unknown	11	1.36	1.42	1.48	0.04	12	1.09	1.25	1.31	0.06
Horizon F	1	–	1.55	–	–	1	–	1.26	–	–
Horizon H	2	1.30	1.33	1.35	–	2	1.17	1.18	1.19	–
Horizon I	32	1.27	1.43	1.58	0.07	33	1.11	1.27	1.37	0.05
Horizon J	24	1.33	1.43	1.56	0.05	24	1.18	1.26	1.32	0.04
Horizon K	17	1.34	1.44	1.59	0.06	17	1.17	1.25	1.33	0.05
Horizon L	15	1.29	1.43	1.53	0.06	15	1.15	1.24	1.30	0.05
Suse Quarry (West Fissure)*	18	1.28	1.41	1.52	0.06	18	1.16	1.23	1.32	0.04
LATE PLEISTOCENE										
Suse Quarry (East Fissure)*	7	1.29	1.37	1.42	0.04	7	1.18	1.21	1.24	0.02
Kumaishi-do Cave										
F_1, F_2 and F_4	10	1.32	1.40	1.49	0.06	10	1.15	1.22	1.28	0.04
F_3	47	1.23	1.36	1.48	0.06	47	1.09	1.18	1.29	0.05
Kannondo Cave Site										
Horizon M (upper)	10	1.31	1.41	1.54	0.07	9	1.12	1.22	1.29	0.05
Horizon M (lower)	14	1.30	1.38	1.52	0.06	14	1.16	1.22	1.31	0.04
Horizon N	4	1.33	1.39	1.48	–	3	1.12	1.17	1.24	–
Horizon O (upper)	2	1.34	1.42	1.49	–	2	1.20	1.20	1.21	–
Horizon O (lower)	3	1.32	1.44	1.52	–	4	1.14	1.18	1.23	–
Horizon P	4	1.28	1.43	1.50	–	4	1.11	1.22	1.30	–
Yage Quarry**										
Site 2	1	–	1.34	–	–	1	–	1.24	–	–
Site 4	4	1.19	1.33	1.42	–	4	1.15	1.19	1.22	–
Sugi-ana Cave	10	1.31	1.38	1.47	0.05	11	1.18	1.24	1.31	0.05
Aisawa Quarry	3	1.45	1.49	1.53	–	3	1.22	1.23	1.25	–
Loc.2 of Ube Kosan Quarry	1	–	1.35	–	–	1	–	1.12	–	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 1	1	–	1.39	–	–	1	–	1.22	–	–
Layer 2	4	1.33	1.39	1.49	–	4	1.18	1.22	1.25	–
Layer 3	2	1.38	1.39	1.39	–	2	1.16	1.23	1.30	–
Loc.3 of Ube Kosan Quarry										
Layer 18	14	1.22	1.39	1.48	0.08	15	1.09	1.21	1.32	0.06
Layer 17	5	1.31	1.36	1.39	0.03	5	1.16	1.21	1.32	0.06
Layer 3	25	1.24	1.39	1.49	0.06	25	1.13	1.20	1.29	0.04
Layer 1	20	1.22	1.36	1.47	0.08	20	1.14	1.19	1.30	0.04
Loc.4 of Ube Kosan Quarry	23	1.24	1.37	1.49	0.08	23	1.09	1.20	1.36	0.06

Table 95. Measurements of M_3 of *Apodemus speciosus*. * MATSUHASHI Collection, ** partly MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	3	1.18	1.20	1.23	–	3	1.08	1.11	1.16	–
Nopporo	2	1.17	1.19	1.21	–	2	1.04	1.06	1.07	–
Otaki	2	1.09	1.12	1.15	–	2	1.00	1.01	1.03	–
HONSHU										
Sugaya	1	–	1.09	–	–	1	–	1.02	–	–
Nikko	2	1.08	1.14	1.21	–	2	1.00	1.05	1.09	–
Nojiri-ko	2	1.04	1.10	1.15	–	2	0.98	1.00	1.02	–
Myogata	19	1.04	1.13	1.19	0.03	19	1.00	1.03	1.08	0.02
Gujohachiman	7	1.03	1.10	1.20	0.05	7	0.93	1.00	1.07	0.05
Ikeda	8	1.03	1.09	1.12	0.03	8	0.95	0.99	1.05	0.03
Mikawa Heights	29	1.07	1.13	1.21	0.04	29	0.90	1.02	1.09	0.04
Mineyama	3	1.13	1.14	1.15	–	3	0.96	0.98	0.99	–
Taishaku	1	–	1.16	–	–	1	–	1.07	–	–
Akiyoshi	10	1.01	1.11	1.22	0.06	10	0.96	1.02	1.08	0.04
HOLOCENE										
Husen-ana Cave	5	1.04	1.09	1.15	0.04	5	0.98	1.02	1.08	0.04
Tanuki-ana Cave (Layer 2)	1	–	1.20	–	–	1	–	1.00	–	–
Kannondo Cave Site										
Horizon unknown	7	1.07	1.15	1.20	0.04	7	0.95	1.03	1.11	0.05
Horizon F	1	–	1.16	–	–	1	–	1.05	–	–
Horizon H	2	1.08	1.11	1.13	–	1	–	0.98	–	–
Horizon I	20	1.07	1.17	1.24	0.05	20	0.99	1.06	1.21	0.05
Horizon J	18	1.00	1.17	1.31	0.07	18	0.93	1.05	1.16	0.05
Horizon K	11	1.08	1.16	1.21	0.04	10	0.89	1.03	1.11	0.06
Horizon L	10	1.06	1.16	1.24	0.05	11	0.90	1.01	1.09	0.05
Suse Quarry (West Fissure)*	11	0.96	1.11	1.17	0.06	11	0.97	1.03	1.08	0.03
LATE PLEISTOCENE										
Suse Quarry (East Fissure)*	3	1.06	1.08	1.09	–	3	0.98	0.99	0.99	–
Kumaishi-do Cave										
F_1, F_2 and F_4	6	1.01	1.07	1.10	0.03	6	0.97	1.00	1.05	0.03
F_3	26	1.04	1.11	1.20	0.04	26	0.92	1.01	1.07	0.04
Kannondo Cave Site										
Horizon M (upper)	4	1.16	1.18	1.19	–	4	1.01	1.02	1.03	–
Horizon M (lower)	3	1.08	1.13	1.21	–	3	0.98	0.99	1.01	–
Horizon N	5	1.04	1.08	1.14	0.05	5	0.92	1.00	1.07	0.05
Horizon O (upper)	2	1.10	1.10	1.11	–	2	0.97	0.98	0.99	–
Horizon O (lower)	3	0.94	1.09	1.15	–	3	0.93	1.00	1.07	–
Yage Quarry**										
Site 2	1	–	1.02	–	–	1	–	1.03	–	–
Site 4	2	1.16	1.16	1.16	–	2	1.01	1.02	1.03	–
Sugi-ana Cave	1	–	1.13	–	–	1	–	0.99	–	–
Aisawa Quarry	1	–	1.08	–	–	1	–	0.96	–	–
Loc.2 of Ube Kosan Quarry	1	–	1.07	–	–	1	–	0.88	–	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	3	1.09	1.13	1.17	–	3	0.96	1.00	1.02	–
Loc.3 of Ube Kosan Quarry										
Layer 18	9	1.07	1.13	1.20	0.05	9	0.95	1.02	1.10	0.04
Layer 17	2	1.08	1.16	1.23	–	2	0.97	1.04	1.11	–
Layer 3	19	1.00	1.13	1.26	0.06	19	0.96	1.01	1.08	0.03
Layer 1	24	1.03	1.11	1.20	0.05	24	0.93	0.98	1.08	0.04
Loc.4 of Ube Kosan Quarry	13	1.02	1.13	1.18	0.05	13	0.94	1.00	1.04	0.03

Early Pleistocene *Apodemus* in China. In accordance with the description and illustration of TEILHARD (1940), this form is included in the range of the size variation of the present fossils. However the following differential dental characters are also observable in TEILHARD's figure (Fig. 35): (1) In M^1, the posterostyle is rather reduced, and the posterior cingulum is absent; (2) in M^2, the labial anterocone is well-developed; (3) M^3 has a peculiar pattern with two transverse laminas. The characters (1) and (2) are usually invisible in the present fossils. As regards (3), the pattern is entirely different from that of the present fossils.

Among the Middle Pleistocene records of *Apodemus*, comparable descriptions with the present fossils are given only in YOUNG (1934; "*A. sylvaticus*" from Locality 1 of Choukoutien) and PEI (1936; "*A. sylvaticus*" from Locality 3 of Choukoutien). Judging from YOUNG's figure, "*A. sylvaticus*" from Locality 1 seems to comprise at least two forms, namely larger and smaller forms. The smaller form is rather similar to *A. peninsulae* in having "*giliacus* type" patterns in the upper molars, and in the position of the posterior ends of the incisive foramina. The larger form is characterized by the well-developed prestyles and precingulum of M^1, absence or weakness of the posterior cingulum in M^1 and M^2, well-developed labial anterocone of M^2, and M^3 pattern of "*giliacus* type" or "*speciosus* type." The buccal accessory cusps of M_1 is remarkably weak in both forms. As regards their sizes, the smaller form is somewhat smaller than the present fossils, whereas the larger form is as large as the fossils. Therefore, both forms are distinguishable from the present fossils by most of these characters.

"*A. sylvaticus*" from Locality 3 of Choukoutien is nearly as large as, or somewhat smaller than the present fossils. However this form can be discriminated from them by the number of roots in M^1, complete absence of the labial anterocone in M^2 and peculiar pattern of M^3, judging from the figure by PEI (1936; Fig. 32).

In addition to these, the Middle Pleistocene fossils from Luochuan, Gongwangling, Chenchiaou and Koloshan are represented only by mandibles, lower molars or incisors. Since these parts are not diagnostic, the close comparisons with the present fossils are impossible.

The Late Pleistocene fossils of *Apodemus* are known from Sanjiacun. They are referred to *A. draco* and *A. latronum* (QIU *et al.*, 1984). The fossil of *A. draco* is smaller than the present Japanese fossils. It is also distinguishable from them in having a well-developed labial anterocone of M^2 and in having the M^3 pattern rather similar to "*argenteus* type." The fossil of *A. latronum* is included in the range of the size variation of the present fossils. Its molar patterns are somewhat near to those of the present fossils. However some minor differences between them are also observable in the degree of the development of the posterior cingulums of M^1 and M^2, and of the labial anterocone of M^2.

The descriptions of the other Late Pleistocene *Apodemus* from the Upper Cave of Choukoutien and Yunshui Cave are too insufficient to compare with the present fossils. However M_2 from the latter locality is clearly smaller than that of the present fossils, and has nearly the same size as smaller individuals of *A. giliacus* or larger individuals of *A. argenteus*.

Comparisons with the European fossil species ——

The Pliocene to Early Pleistocene fossil species of *Apodemus* are represented by *A. jeanteti* MICHAUX and *A. dominans* KRETZOI which arose in common from *Parapodemus gaudryi* (DAMES) in the Early Pliocene. *A. jeanteti* is a large-sized species and is considered to be the ancestor of *A. mystacinus* (MICHAUX and PASQUIER, 1974; CHALINE and

MEIN, 1979). According to the description and figure by MICHAUX (1967), *A. jeanteti* differs from the present fossils by its larger size and by the absence or strong reduction of the medial anteroconid in M_1.

On the other hand, *A. dominans* is considered to be the common ancestor of *A. flavicollis* and *A. sylvaticus* (MICHAUX and PASQUIER, 1974; CHALINE and MEIN, 1979). The size of this species is considerably variable, but approximately coincident with the range of the present fossils. In comparison with the descriptions of *A. dominans* and some allied forms from various localities in Europe (SULIMSKI, 1964; BRUIJN *et al.*, 1970; MEULEN, 1973; BRUIJN and MEULEN 1975; SEN, 1977; WEERD, 1979; WEERD *et al.*, 1982), the present fossils are similar to this species in having three-rooted M^1 and M^2, and in several aspects of molar patterns. However some differences are also observable. *A. dominans* differs from the present fossils in the frequency of the appearance of the posterior spur of the labial anterocone of M^1 and in the degree of the development of the labial anterocone of M^2.

Concluding remarks on the comparisons ——

Summarizing the comparisons, it can be stated that the present Japanese fossils are more or less different from the living and fossil species of *Apodemus* compared above. Therefore the identification of these fossils as *A. speciosus* is firmly suppored.

Discussion

The taxonomic position of the living *A. speciosus* is still controversial. Many previous authors have offered several different opinions on this problem and on the geographical distribution of this species. In a series of his work (1905b; 1906b; 1907; 1908a, b, c; 1911a, b; 1912a, b), THOMAS considered that *A. speciosus* was distributed in Japan, Sakhalin, Korea and vast areas of China, and described *navigator, ainu, giliacus, peninsulae, latronum, orestes* and *chevrieri* as its subspecies. His opinion was partly followed by several later authors. However TOKUDA (1941b) expressed the different opinion that *A. speciosus* was restricted to Honshu, Shikoku, Kyushu and their adjacent small islands, and he gave a specific rank to *ainu* which included *ainu* (*sensu stricto*) of Hokkaido and *peninsulae* of Korea. On the other hand, *A. speciosus* was regarded as an endemic species to Japan (Hokkaido, Honshu, Shikoku, Kyushu and their adjacent small islands) by ALLEN (1940), ELLERMAN and MORRISON-SCOTT (1951) and IMAIZUMI (1960). In 1974, TSUCHIYA found two types of *A. speciosus* with different chromosome numbers ($2n=46$ and 48) in Japan. The type with $2n=48$ is distributed in Hokkaido and northeastern part of Honshu, but the type with $2n=46$ is in southwestern part of Honshu, Shikoku and Kyushu. From this fact, VORONTSOV *et al.* (1977) regarded both types as independent species, and called the former *A. speciosus* and the latter *A. navigator*. The recent authors, however, did not agree with their opinion, but considered *A. speciosus* as an endemic species to Japan ranging from Hokkaido to Kyushu (CORBET, 1978; HONACKI *et al.*, 1982; ABE, 1984). The present author follows such a recent view, because it seems to be most reasonable from his own viewpoints on the osteological and dental characters of this species.

As already described, *A. speciosus* has flourished in Japan since the Middle Pleistocene. However comparable forms with this species are not found in any fossil records of the Late and Middle Pleistocene of China which are available for the present author. Therefore the distribution of *A. speciosus* has been probably restricted to Japan during in this period.

The present study indicates that the temporal morphological changes since the Middle Pleistocene are generally slight in this species. Even the Middle Pleistocene fossils which are considered to be the earliest in geological age of all the materials available for the present study are quite similar to the living *A. speciosus*. Therefore the origin of this species is assumed to be much earlier. The fossil evidences in Europe suggest that the evolutionary rates of the species of *Apodemus* are much slower than those of voles. For example, it is considered that the genus *Apodemus* arose from *Parapodemus* in the Early Pliocene, and the living European species such as *A. mystacinus, A. flavicollis* and *A. sylvaticus* first appeared in the Early Pleistocene. If the evolutionary rate in the lineage of *A. speciosus* was similar to those of the European species, *A. speciosus* possibly derived from its hypothetical ancestor in the Early Pleistocene or somewhat earlier periods. This ancestor may have resembled *A. dominans* of the Pliocene to Early Pleistocene of Europe. Because the Early Pleistocene records of *Apodemus* in East Asia are too scarce to discuss the relationship with *A. speciosus*, the origin and early history of this species are still unknown. In order to solve this problem, it is necessary to find out new materials of this period.

As regards the knowledge of the living *Apodemus*, ZIMMERMANN (1962) allocated this species to the subgenus *Alsomys*, the eastern group of *Apodemus*, as well as *A. peninsulae, A. latronum, A. semotus* and *A. draco*. These species of *Alsomys* seem to be divided into two groups by the morphological similarities, namely "*speciosus-peninsulae*" group and "*latronum-semotus-draco*" group. If such a subdivision is acceptable, *A. speciosus* originated from a common ancestor to *A. peninsulae*. Although the intraspecific changes since the Middle Pleistocene are generally slight in *A. speciosus* as mentioned above, the tendencies of the reductions in size and in the posterior cingulums of M^1 and M^2 are observable from the recent to Middle Pleistocene populations. If such tendencies can be traced back to the Early Pleistocene, *A. speciosus* of that time might approach the living *A. peninsulae* in these characters (but the Early Pleistocene ancestor of the latter species is also unknown).

Nevertheless, such discussions on the ancestory of *A. speciosus* are only tentative and include many speculations. These attribute to the instability in the classification of the living *A. speciosus* and its allied species, and the extreme scarcity of the Early Pleistocene or Pliocene fossils of *Apodemus* in East Asia. Further accumulation of palaeontological, morphological and cytotaxonomical data is expected.

Apodemus argenteus (TEMMINCK, 1844)

(Figs. 180–182)

Mus argenteus, TEMMINCK 1844, *Fauna Japonica, Mamm.,* 51.

Synonym (*living forms*) ——

Micromys geisha; THOMAS 1905a, *Ann. Mag. Nat. Hist.,* Ser. 7, **15,** 491–493.

Micromys geisha THOMAS; THOMAS 1905b, *Proc. Zool. Soc. London,* **1905,** 350–351, 359, 363. (including *M. geisha hokkaidi, M. g. celatus* and *M. g. yakui*).

Apodemus geisha sagax; THOMAS 1908, *Proc. Zool. Soc. London,* **1908,** 54.

Apodemus geisha geisha (THOMAS), *A. g. sagax* THOMAS, *A. g. celatus* (THOMAS) and *A. g. yakui* (THOMAS); AOKI 1915, *Nipponsan Nezumika* (*Japanese Muridae*), 26–31.

Apodemus geisha geisha (THOMAS), *A. g. hokkaidi* (THOMAS), *A. g. celatus* (THOMAS), *A. g. sagax* THOMAS and *A. g. yakui* (THOMAS); KISHIDA 1924, *Honyudobutsu Zukai* (*Monogr. Japanese Mamm.*), 120–124.

Apodemus geisha geisha (THOMAS) and *A. g. hokkaidi* (THOMAS); WATANABE 1937, *Occ. Pap. Ibaraki Agr. St.,* (2), 34–39.

Apodemus geisha geisha (THOMAS), *A. g. hokkaidi* (THOMAS), *A. g. celatus* (THOMAS), *A. g. sagax* THOMAS, *A. g. yakui* (THOMAS) and *A. g. tanei* KURODA; KURODA 1940, *Monogr. Japanese Mamm.,* 117–120.

Apodemus geisha (THOMAS); TOKUDA 1941, *Trans. Biogeogr. Soc. Japan,* **4,** 91–93. (including *A. g.* var. *celatus*)

Apodemus geisha (THOMAS); IMAIZUMI 1949, *Nat. Hist. Japanese Mamm.,* 260–263.

Apodemus sylvaticus argenteus TEMMINCK, *A. s. celatus* THOMAS and *A. s. sagax* THOMAS; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian Mammals,* 570–571.

Apodemus sylvaticus argenteus (TEMMINCK & SCHLEGEL), *A. s. sagax* THOMAS, *A. s. hokkaidi* (THOMAS), *A. s. celatus* (THOMAS), *A. s. yakui* (THOMAS) and *A. s. tanei* KURODA; KURODA 1953, *Nippon Jurui Zusetsu* (*Monogr. Japanese Mamm.*), 82.

Apodemus argenteus; JONES and IMAIZUMI 1956, *Jour. Mammal.,* **37,** 273–274.

Apodemus argenteus TEMMINCK; IMAIZUMI 1960, *Coloured Illustr. Mamm. Japan,* 145–147.

Apodemus argenteus (TEMMINCK); KOBAYASHI and HAYATA 1971, *Annot. Zool. Japon.,* **44,** 236–237.

Apodemus argenteus TEMMINCK; VORONTSOV *et al.* 1977, *Zool. Zhur.,* **56,** 446.

Apodemus argenteus; CORBET 1978, *The Mammals of the Palaearctic Region,* 136.

Synonym (*fossil forms*) ——

Apodemus geisha (THOMAS); SHIKAMA and OKAFUJI 1958, *Sci. Rep. Yokohama Nat. Univ.,* Sect. 2, (7), 56, 58, 67, 69; from Koziki-ana Cave, Makurazino-ana Cave, Mizushimano-ana Cave and Iriminoana Cave.

Mus cfr. *musculus molossinus* TEMMINCK; NAORA 1972, *Kodai-iseki Hakkutsu-no Sekitsui-dobutsu-itai* (*Vertebrate Remains from Archaeological Sites*), 181–182; from Shiriya Quarry.

Apodemus argenteus (TEMMINCK); KOWALSKI and HASEGAWA 1976, *Bull. Nat. Sci. Mus.,* Ser. C, **2,** 40, 42–43; from Ikumo Quarry, Ando Quarry, Shiraiwa Mine, Shiriya Quarry, Takanosuzawa Cave, Miyata First Cave, Miyata Second Cave, Okada Quarry, Aizawa (=Yoshizawa), Ushikawa Mine, Shikimizu Quarry and Makurazino-ana Cave.

Apodemus argenteus (TEMMINCK); KAWAMURA 1977, *Fossil Club Bull.,* (14), 7; from Kumaishi-do Cave.

Apodemus argenteus (TEMMINCK); KAWAMURA 1978, 1979, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre,* **1,** 57; **2,** 46; from the Holocene horizons of Kannondo Cave Site.

Apodemus argenteus TEMMINCK; TOMIDA 1978, *Bull. Mizunami Fossil Mus.,* (5), 127; from Yage Quarry.

Apodemus argenteus (TEMMINCK); KAWAMURA 1980, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre,* **3,** 65; from the Late Pleistocene horizons of Kannondo Cave Site.

Apodemus argenteus (TEMMINCK); KAWAMURA and TAMIYA 1980, *Bull. Akiyoshi-dai Mus. Nat. Hist.,* (15), 32; from Tanuki-ana Cave.

Apodemus argenteus (TEMMINCK); KAWAMURA and KAJIURA 1980, *Jour. Speleol. Soc. Japan,* **5,** 53; from Sugi-ana Cave.

Apodemus argenteus (TEMMINCK); KAWAMURA 1982, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre,*

5, 60; from the Late Pleistocene horizons of Kannondo Cave Site.

Apodemus argenteus (Temminck); Okumura *et al.* 1982, *Earth Sci.*, **36,** 216; from Kumaishi-do Cave.

Apodemus argenteus; Kawamura and Sotsuka 1984, *Bull. Kitakyushu Mus. Nat. Hist.*, (5), 172; from Seiryukutsu Cave, Ninjinkubo First Cave, Yakubono-ana Cave, Ojika-do Cave and Yoshigatani Third Cave.

Apodemus argenteus (Temminck); Kawamura *et al.* 1986, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre,* **9,** 71; from the Late Pleistocene horizons of Kannondo Cave Site.

Materials ——

MIDDLE PLEISTOCENE LOCALITIES

Ikumo Quarry

1 mandible with I, M_2 and M_3 (ASM 700009); 1 mandible without teeth (ASM 700010); 1 isolated M_1 (ASM 700011).

Locality 4 of Ube Kosan Quarry

91 isolated M^1 (ASM 701431–701520, 701531); 75 isolated M^2 (ASM 701541–701615); 25 isolated M^3 (ASM 701625–701649); 117 isolated M_1 (ASM 701680–701796); 104 isolated M_2 (ASM 701817–701920); 53 isolated M_3 (ASM 701938–701990).

Locality 3 of Ube Kosan Quarry

Layer 1: 1 maxilla with M^1, M^2 and M^3 (KUJC97179); 2 maxillae with M^1 and M^2 (KUJC97181, 97183); 1 maxilla with M^2 and M^3 (KUJC97184); 3 maxillae with M^1 (KUJC97177, 97178, 97182); 3 maxillae with M^2 (KUJC97185–97187); 2 maxillae without teeth (KUJC97260, 97261); 31 isolated M^1 (KUJC97163, 97228–97257); 24 isolated M^2 (KUJC97435–97458); 9 isolated M^3 (KUJC97566–97573, 97631); 1 mandible with M_1, M_2 and M_3 (KUJC 97193); 2 mandibles with M_1 and M_2 (KUJC97192, 97197); 1 mandible with M_1 (KUJC 97196); 3 mandibles with M_2 (KUJC97191, 97194, 97195); 1 mandible without teeth (KUJC 97262); 27 isolated M_1 (KUJC97650–97675, 98045); 20 isolated M_2 (KUJC97168, 97827–97845); 19 isolated M_3 (KUJC97957–97974, 98046).

Layer 3: 1 maxilla with M^2 (KUJC97267); 40 isolated M^1 (KUJC97309–97348); 25 isolated M^2 (KUJC97483–97506, 98050); 14 isolated M^3 (KUJC97598–97611); 1 mandible with I, M_1, M_2 and M_3 (KUJC97282); 2 mandibles with I, M_1 and M_2 (KUJC97278, 97283); 1 mandible with I and M_1 (KUJC97281); 1 mandible with I and M_2 (KUJC97280); 2 mandibles with M_1 (KUJC97279, 97284); 1 mandible with M_2 (KUJC97285); 34 isolated M_1 (KUJC 97697–97729, 98051); 29 isolated M_2 (KUJC97863–97891); 31 isolated M_3 (KUJC97992–98022).

Layer 4: 1 mandible without teeth (KUJC98060).

Layer 8: 1 maxilla without teeth (KUJC98059).

Layer 17: 1 maxilla with M^1 (KUJC97371); 14 isolated M^1 (KUJC97359–97370, 97373, 98052); 4 isolated M^2 (KUJC97512–97514, 98053); 1 isolated M^3 (KUJC97614); 1 mandible with M_1, M_2 and M_3 (KUJC97372); 2 mandibles with I, M_1 and M_2 (KUJC97353, 97354); 12 isolated M_1 (KUJC97738–97749); 5 isolated M_2 (KUJC97896–97900); 2 isolated M_3 (KUJC98024, 98025).

Layer 18: 1 maxilla with M^2 (KUJC97386); 26 isolated M^1 (KUJC97379–97385, 97401–97418, 98054); 11 isolated M^2 (KUJC97521, 97522, 97540–97548); 3 isolated M^3 (KUJC97628–97630); 1 mandible with M_1 (KUJC97387); 1 mandible with M_2 (KUJC97375); 41 isolated M_1 (KUJC97760–97772, 97785–97812); 18 isolated M_2 (KUJC97905–97910, 97922–97933); 9 isolated M_3 (KUJC98031, 98036–98043).

In addition to these materials, numerous unnumbered specimens such as maxillary fragments, mandibles and isolated teeth are obtained from all the layers except Layer 7.

Locality 1 of Ube Kosan Quarry

Layer 3: 3 isolated M^1 (ASM 702059–702061).

Layer 2: 5 isolated M^1 (ASM 702027–702031); 1 isolated M^2 (ASM 702034); 1 mandible with I (ASM 702052); 1 mandible without teeth (ASM 702053); 2 isolated M_1 (ASM 702040, 702041); 3 isolated M_2 (ASM 702045–702047); 1 isolated M_3 (ASM 702051).

Layer 1: 1 isolated M_1 (ASM 702024).

LATE PLEISTOCENE LOCALITIES

Locality 2 of Ube Kosan Quarry

5 isolated M^2 (ASM 702993–702997); 2 isolated M_2 (ASM 702998, 702999); 1 isolated M_3 (ASM 703000).

Aisawa Quarry

3 isolated M^1 (KUJC 100425–100427); 1 mandible with I and M_2 (KUJC 100428).

Sugi-ana Cave

3 maxillae with M^1 and M^2 (KUJC 100429–100431); 3 maxillae with M^2 and M^3 (KUJC 100432–100434); 2 maxillae with M^1 (KUJC 100435, 100436); 4 maxillae with M^2 (KUJC 100437–100440); 1 maxilla with M^3 (KUJC 100441); 20 maxillae without teeth (KUJC 100442–100461); 9 isolated M^1 (KUJC 100462–100470); 3 isolated M^2 (KUJC 100471–100473); 3 mandibles with I, M_1, M_2 and M_3 (KUJC 100474–100476); 1 mandible with M_1, M_2 and M_3 (KUJC 100477); 3 mandibles with I, M_1 and M_2 (KUJC 100478–100480); 2 mandibles with M_1 and M_2 (KUJC 100481, 100482); 2 mandibles with I and M_1(KUJC 100483, 100484); 7 mandibles with M_1 (KUJC 100485–100491); 17 mandibles with I (KUJC 100492–100508); 20 mandibles without teeth (KUJC 100509–100528); 15 isolated M_1 (KUJC 100529–100543); 4 isolated M_2 (KUJC 100544–100547); 3 isolated M_3 (KUJC 100548–100550).

Yage Quarry

Site 2 (unnumbered specimens of the MATSUHASHI Collection): 1 mandible with I and M_1; 1 mandible with I.

Site 4: 1 isolated M^1 (KUJC 100551); 1 isolated M_2 (KUJC 100552).

Seiryukutsu Cave

1 mandible with I, M_1 and M_2 (KMNH VP 300,021); 1 mandible with M_1 and M_2 (KMNH VP 300,022).

Kannondo Cave Site (Late Pleistocene horizons; specimen numbers are prefixed by HUA)

Horizon P: 2 maxillae with M^1 (K 04027, 04028); 3 isolated M^1 (K 04029–04031); 1 isolated M^3 (K 04032); 3 mandibles without teeth (K 04033–04035); 4 isolated M_1 (K 04036–04039); 2 isolated M_2 (K 04040, 04041); 3 isolated M_3 (K 04042–04044).

Horizon O (lower part): 1 maxilla with M^1 (K 04045); 3 maxillae without teeth (K 04046–04048); 5 isolated M^1 (K 04049–04053); 5 isolated M^2 (K 04054–04058); 2 isolated M^3 (K 04059, 04060); 2 mandibles with I, M_1 and M_2 (K 04061, 04062); 2 mandibles with M_1 and M_2 (K 04063, 04064); 1 mandible with I and M_1 (K 04065); 2 mandibles with M_1 (K 04066, 04067); 1 mandible with M_2(K 04068); 2 mandibles with I (K 04069, 04070); 6 mandibles without teeth (K 04071–04076); 10 isolated M_1 (K 04077–04086); 6 isolated M_2 (K 04087–04092); 1 isolated M_3 (K 04093).

Horizon O (upper part): 2 maxillae with M^1 and M^2 (K 00300, 04094); 3 maxillae with M^1 (K 00301–00303); 1 maxilla without teeth (K 00304); 2 isolated M^1 (K 00305, 00306); 1 mandible with M_1 and M_2 (K 04095); 1 mandible with M_1 (K 00307); 4 mandibles without teeth (K 00308–00310, 04096); 9 isolated M_1 (K 00311–00318, 04097).

Horizon N: 2 maxillae with M^1 and M^2 (K 00193, 00272); 1 maxilla with M^1 (K 00212); 1 maxilla with M^3 (K 00246); 1 maxilla without teeth (K 00263); 1 isolated M^1 (K 00213); 1 mandible with I, M_1, M_2 and M_3 (K 04098); 1 mandible with I, M_1 and M_2 (K 00209); 1 mandible with M_1 and M_2 (K 00247); 1 mandible with M_1 (K 00248); 1 mandible with M_2 (K 00264); 11 mandibles without teeth (K 00210, 00214–00217, 00249–00252, 00273, 00274); 14 isolated M_1 (K 00194, 00195, 00199, 00205, 00220, 00253–00255, 00265–00268, 00275, 00276); 6 isolated M_2 (K 00200, 00201, 00211, 00218, 00219, 00269); 1 isolated M_3 (K 00270).

Horizon M (lower part): 3 maxillae with M^1 and M^2 (K 00102, 00104, 00177); 1 maxilla with M^2 (K 00103); 2 isolated M^1 (K 00136, 00178); 1 mandible with I, M_1 and M_2 (K 00121); 1 mandible with M_1 and M_2 (K 00118); 1 mandible with M_1 (K 00122); 1 mandible with M_2 (K 00119); 2 mandibles with I (K 00120, 00123); 4 mandibles without teeth (K 00124–00126, 00187); 6 isolated M_1 (K 00146–00148, 00171, 00176, 00188); 1 isolated M_2 (K 00156).

Horizon M (upper part): 1 maxilla with M^2 and M^3 (K 00014); 3 maxillae with M^1 (K 00009, 00012, 00013); 1 maxilla with M^2 (K 00010); 5 maxillae without teeth (K 00011, 00015–00018); 2 isolated M^1 (K 00062, 00063); 1 isolated M^3 (K 00067); 1 mandible with I, M_1, M_2

and M_3 (K00031); 1 mandible with M_1, M_2 and M_3 (K00032); 1 mandible with I, M_2 and M_3 (K00033); 5 mandibles with M_1 and M_2 (K00034–00036, 00043, 00044); 1 mandible with M_1 (K00045); 1 mandible with M_2 (K00046); 3 mandibles with I (K00037, 00038, 00047); 9 mandibles without teeth (K00039–00042, 00048–00052); 1 isolated M_1 (K00085); 1 isolated M_3 (K00095).

In addition to these materials, numerous specimens such as maxillary fragments, mandibles and isolated teeth are also obtained from all the horizons.

Kumaishi-do Cave

F_3: 1 maxilla with M^1, M^2 and M^3 (YKS 02153); 3 maxillae with M^1 (YKS 02019, 02140, 02212); 1 maxilla without teeth (YKS 02164); 23 isolated M^1 (YKS 02018, 02027, 02029, 02031, 02062, 02106, 02116, 02125, 02162, 02167, 02190, 02196, 02204, 02215, 02217, 02220, 02229, 02288–02290, 02339–02341); 13 isolated M^2 (YKS 02049, 02101, 02156, 02201, 02202, 02225, 02274, 02306–02308, 02352–02354); 4 isolated M^3 (YKS 02100, 02364, 02365, 02372); 1 mandible with I, M_1 and M_2 (YKS 02128); 1 mandible with M_1 and M_2 (YKS 02016); 1 mandible with I and M_2 (YKS 02243); 2 mandibles with M_2 (YKS 02148, 02362); 1 mandible with I (YKS 02158); 1 mandible without teeth (YKS 04233); 21 isolated M_1 (YKS 02036, 02063, 02072, 02092, 02095, 02096, 02208, 02219, 02234, 02251, 02252, 02254–02257, 02301, 02302, 02344–02346, 02388); 15 isolated M_2 (YKS 02046, 02050, 02055, 02223, 02224, 02260, 02261, 02319–02323, 02359–02361); 7 isolated M_3 (YKS 02103, 02171, 02173, 02330, 02375, 02378, 02379).

F_1, F_2 and F_4: 1 maxilla with M^1 (YKS 02140); 2 isolated M^1 (YKS 02001, 02002); 1 isolated M^2 (YKS 02131); 1 mandible with I, M_1, M_2 and M_3 (YKS 02132); 5 isolated M_1 (YKS 00406, 02008, 02133, 02137, 02181); 1 isolated M_2 (YKS 02141).

Suse Quarry (East Fissure; unnumbered specimens of the Matsuhashi Collection)

2 mandibles with I and M_1; 1 mandible with I and M_2; 1 mandible with I.

HOLOCENE LOCALITIES

Suse Quarry (West Fissure; unnumbered specimen of the Matsuhashi Collection)

1 mandible with I and M_1.

Kannondo Cave Site (Holocene horizons; specimen numbers are prefixed by HUA)

Horizon L: 1 mandible with I (K04099).

Horizon K: 1 mandible with I, M_1, M_2 and M_3 (K04100); 1 mandible with I, M_1 and M_2 (K04101); 1 mandible with M_1 and M_2 (K04102).

Horizon J: 1 maxilla without teeth (K04103); 1 mandible with I, M_1, M_2 and M_3 (K04104); 3 mandibles with I, M_1 and M_2 (K04105–04107); 1 mandible with M_1 (K04108); 1 mandible with I (K04109); 2 mandibles without teeth (K04110, 04111).

Horizon I: 1 maxilla with M^1 and M^2 (K04112); 1 maxilla with M^1 (K04113); 2 mandibles with I, M_1, M_2 and M_3 (K04114, 04115); 2 mandibles with I, M_1 and M_2 (K04116, 04117); 2 mandibles with M_1 and M_2 (K04118, 04119); 3 mandibles with I (K04120–04122); 3 mandibles without teeth (K04123–04125).

Horizon F: 1 mandible with I (K04126).

Horizon C: 1 mandible without teeth (K04127).

Horizon unknown: 1 isolated M^1 (K04128); 1 mandible with I, M_1 and M_2 (K04129); 1 mandible with I and M_1 (K04130); 1 mandible with M_2 (K04131); 1 mandible with I (K04132); 1 mandible without teeth (K04133); 1 isolated M_1 (K04134); 1 isolated M_2 (K04135).

Domen Cave Site (Horizon V; specimen numbers are prefixed by HUA)

1 maxilla with M^1 (D00112); 1 maxilla without teeth (D00113); 3 isolated M^1 (D00114–00116); 3 isolated M_1 (D00117–00119).

Tanuki-ana Cave

Layer 4: 2 maxillae with M^1, M^2 and M^3 (ASM 703001, 703002); 2 maxillae with M^1 and M^2 (ASM 703003, 703004); 1 maxilla with M^2 and M^3 (ASM 703005); 7 maxillae with M^1 (ASM 703006–703012); 3 maxillae with M^2 (ASM 703013–703015); 1 maxilla with M^3 (ASM 703016); 15 maxillae without teeth (ASM 703017–703031); 28 isolated M^1 (ASM 703032–703059); 9 isolated M^2 (ASM 703060–703068); 2 isolated M^3 (ASM 703069, 703070); 1 mandible with I, M_1, M_2 and M_3 (ASM 703071); 3 mandibles with M_1 and M_2 (ASM 703072–703074); 1 mandible with M_2 and M_3 (ASM 703075); 4 mandibles with M_1 (ASM 703076–

703079); 1 mandible with M_2 (ASM 703080); 2 mandibles with I (ASM 703081, 703082); 34 mandibles without teeth (ASM 703083–703116); 41 isolated M_1 (ASM 703117–703157); 13 isolated M_2 (ASM 703158–703170); 5 isolated M_3 (ASM 703171–703175).

Layer 3: 1 maxilla with M^1, M^2 and M^3 (ASM 703176); 1 maxilla with M^1 and M^2 (ASM 703177); 1 maxilla with M^1 (ASM 703178); 1 maxilla with M^2 (ASM 703179); 2 maxillae without teeth (ASM 703180, 703181); 5 isolated M^1 (ASM 703182–703186); 1 isolated M^2 (ASM 703187); 4 mandibles with M_1 and M_2 (ASM 703188–703191); 1 mandible with M_1 (ASM 703192); 3 mandibles without teeth (ASM 703193–703195); 7 isolated M_1 (ASM 703196–703202); 2 isolated M_2 (ASM 703203, 703204).

Layers 3 to 2: 1 maxilla with M^1 (ASM 703205); 1 maxilla with M^2 (ASM 703206); 2 maxillae without teeth (ASM 703207, 703208); 3 isolated M^1 (ASM 703209–703211); 1 isolated M^2 (ASM 703212); 1 isolated M^3 (ASM 703213); 1 mandible with I, M_1 and M_2 (ASM 703214); 4 mandibles without teeth (ASM 703215–703218); 1 isolated M_1 (ASM 703219); 4 isolated M_2 (ASM 703220–703223); 1 isolated M_3 (ASM 703224).

Layer 2: 2 maxillae with M^1 and M^2 (ASM 703225, 703226); 6 maxillae with M^1 (ASM 703227–703232); 16 maxillae without teeth (ASM 703233–703248); 24 isolated M^1 (ASM 703249–703272); 10 isolated M^2 (ASM 703273–703282); 3 isolated M^3 (ASM 703283–703285); 1 mandible with I, M_1 and M_2 (ASM 703286); 3 mandibles with M_1 and M_2 (ASM 703287–703289); 1 mandible with I and M_2 (ASM 703290); 4 mandibles with M_1 (ASM 703291–703294); 4 mandibles with M_2 (ASM 703295–703298); 3 mandibles with I (ASM 703299–703301); 17 mandibles without teeth (ASM 703302–703318); 23 isolated M_1 (ASM 703319–703341); 12 isolated M_2 (ASM 703342–703353); 5 isolated M_3 (ASM 703354–703358).

Layer 1: 1 maxilla with M^1, M^2 and M^3 (ASM 703359); 1 maxilla with M^1 and M^2 (ASM 703360); 1 maxilla with M^1 (ASM 703361); 2 maxillae without teeth (ASM 703362, 703363); 1 mandible with I, M_1, M_2 and M_3 (ASM 703364); 1 mandible with M_1 (ASM 703365); 1 isolated M_3 (ASM 703366).

Husen-ana Cave

1 maxilla with M^1 and M^2 (ASM 702991); 1 maxilla with M^1 (ASM 702992); 1 isolated M^1 (ASM 702941); 1 mandible with I (ASM 702986); 1 mandible without teeth (ASM 702985); 4 isolated M_1 (ASM 702962–702965); 3 isolated M_2 (ASM 702970–702972).

Yoshigatani Third Cave (unnumbered specimen of the Sotsuka Collection)

1 mandible with I.

Ninjinkubo First Cave (unnumbered specimens of the Sotsuka Collection)

1 maxilla with M^1, M^2 and M^3; 1 maxilla with M^1 and M^2; 1 maxilla with M^1; 5 maxillae without teeth; 3 isolated M^1; 1 mandible with I, M_1, M_2 and M_3; 1 mandible with I, M_1 and M_2; 1 mandible with I, M_1 and M_3; 1 mandible with M_1 and M_2; 1 mandible with I and M_1; 2 mandibles with I and M_2; 17 mandibles with I; 2 mandibles without teeth; 8 isolated M_1; 2 isolated M_2.

Ojika-do Cave (Branch 1; unnumbered specimens of the Sotsuka Collection)

1 maxilla without teeth; 1 mandible with M_1 and M_2; 4 mandibles with I; 1 isolated M_1.

Yakubono-ana Cave (unnumbered specimen of the Sotsuka Collection)

1 fragmental skull with left I, M^1, M^2 and M^3, and right I, M^1 and M^2.

Diagnosis

Size decidedly smaller than that of *A. speciosus*. Rostrum relatively shorter; anterior margin of masseteric plate situated slightly anterior to the upper border of infraorbital foramen in lateral view; lateral ridges absent; diastema of mandible relatively short.

M^1 usually with four roots, but rarely five; its posterior cingulum always well developed, and easily connecting with metacone in early stages of wear; length and width of M^1 usually less than 1.92 and 1.20 mm respectively; M^2 always with four roots; its posterior cingulum well developed as in M^1; its labial anterocone also well developed; length and width of M^2 usually less than 1.25 and 1.10 mm respectively; two laminas of M^3 arranged nearly parallel to the transverse axis of the crown; length and width of M^3 usually less than 0.88 and 0.85 mm respectively. Lower molars almost always with two roots; length and width of M_1 usually less than 1.75 and 1.06 mm respectively; those of M_2 usually less than 1.23 and 1.09 mm respectively; entoconid of M_3 somewhat elongated transversely; length and width of M_3 usually less than 1.03 and 0.93 mm respectively.

Description

The osteological and dental measurements are strikingly smaller than those of *A. speciosus.* The characters of the skull, mandible and molars are generally well coincident with those of *A. speciosus.* However some differences are also found by detailed observations.

Skull ——

The skull remains worthy to describe are very few in the present fossil materials. Their general characters are already described in the diagnosis of this species. However maxillary fragments are rather abundantly obtained. The alveolar pits of M^1 is mostly four in number, because most M^1 have four roots (Fig. 180, A). The anterior pit is the largest of the four. The postero-buccal pit is the second, whereas the two lingual pits are somewhat smaller. The specimens with five pits are rarely found, where the number of the lingual pits increases to be three (Fig. 180, B). Because M^1 with only three roots are very rarely found in the present fossil materials as described below, the number of the alveolar pits must be three in such a case. However the specimens with three alveolar pits are hitherto unknown in the present materials. The alveolar pits of M^2 and M^3 are almost always four and three in number respectively.

M^1 ——

The crown comprises three chevrons. Each chevron is divided into three cusps. The disposition and inclination of these cusps are almost identical with those of *A. speciosus.*

The anterior face of the lingual anterocone is almost always smoothed out. The precingulum is always absent, but the prestyle is very rarely present on this face. The posterior spur of the labial anterocone is generally well-developed. It is stronger and more frequently found than that of *A. speciosus.* In some specimens, such a spur is also found on the posterior face of the anterostyle as in *A. speciosus.* The frequencies of the appearences of these spurs as well as those of the precingulum and prestyle are analysed in the next section. The enteroconule is sometimes found between the anterostyle and lingual anterocone. Only in one out of thousands of the examined specimens, an accessory cusp is observed at the lingual entrance of the valley between the anterior and middle chevrons (KUJC97365 from Layer 17 of Locality 3 of Ube Kosan Quarry).

The valley between the enterostyle and posterostyle is deep and relatively broad, so that it does not disappear until later stages of wear. On the other hand, the

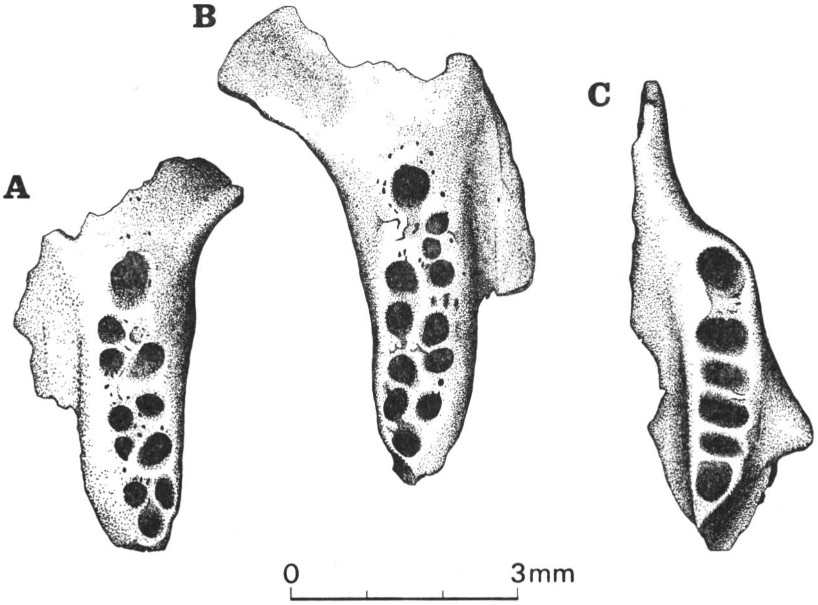


Fig. 180. *Apodemus argenteus.* Alveolar patterns on maxilla (A and B) and mandible (C). A, left maxilla from Layer 8 of Locality 3 of Ube Kosan Quarry (KUJC98059); B, right maxilla from Layer 3 of Tanuki-ana Cave (ASM 703180): C, right mandible from Layer 4 of Locality 3 of Ube Kosan Quarry (KUJC98060).

valley between the paracone and metacone is shallower and narrower, so that the occlusal surfaces of these two cusps are readily confluent.

The posterior cingulum is always well-developed and elongated antero-buccally. It is much stronger than that of *A. speciosus.* However the range of its variation is restricted in comparison with that in *A. speciosus.* When the wear of the crown is advanced, its occlusal surface easily connects with that of the metacone. The small valley between the posterior cingulum and the ridge connecting the hypocone with the metacone is slender but considerably deep. When the metacone-posterior cingulum connection is completed by wear, this valley becomes a closed slit-like pit. Only in one specimen from Layer 3 of Locality 3 of Ube Kosan Quarry (KUJC97321), this valley broadly opens buccally, so that the metacone-posterior cingulum connection is never formed even in later stages of wear. Such a pattern is quite similar to that of *A. speciosus.* On the other hand, only four specimens (KUJC97255 and 97322 from Layers 1 and 3 of Locality 3 of Ube Kosan Quarry; HUA-K00302 and 00306 from the upper part of Horizon O of Kannondo Cave Site) have the pattern of "*giliacus* type" (Fig. 160), where the posterior cingulum connects with the metacone, but the hypocone is separated from the metacone by a distinct valley.

Most specimens have four roots; namely one anterior, two lingual and one

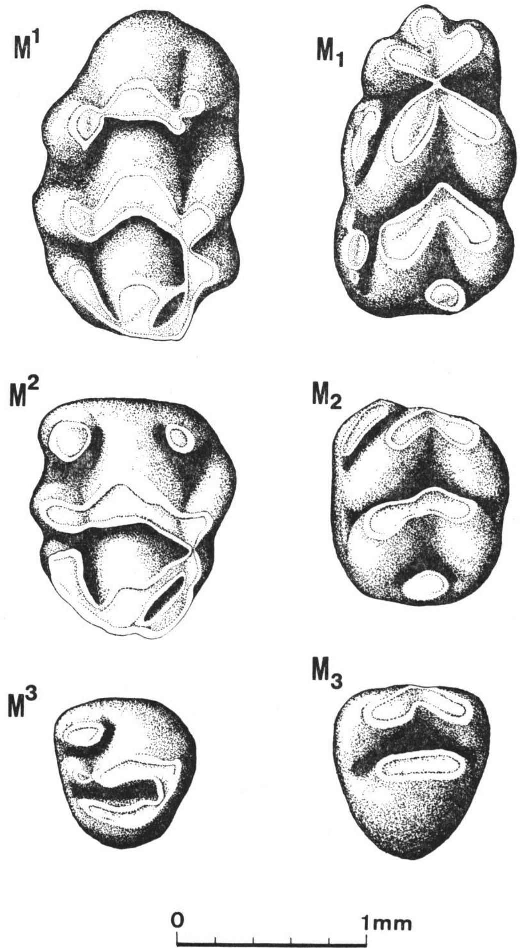


Fig. 181. *Apodemus argenteus*. Occlusal view of the left molars from Locality 3 of Ube Kosan Quarry. M^1, KUJC97230 from Layer 1; M^2, KUJC97438 from Layer 1; M^3, KUJC97606 from Layer 3; M_1, KUJC97738 from Layer 17; M_2, KUJC97837 from Layer 1; M_3, KUJC97959 from Layer 1.

posterior roots (Table 98). These roots are oval in cross section. The anterior root is the largest of the four. The posterior root is slightly smaller than the anterior root. The two lingual roots are closely arranged in each other. Of these two, the anterior one is larger. It is rarely subdivided into two small roots (Table 98). In this case, the total number of roots is five. On the other hand, only in two specimens from Layers 1 and 3 of Locality 3 of Ube Kosan Quarry (KUJC97236 and 97348), the number of roots decreases into three by the fusion of the postero-lingual and posterior roots, or the antero-lingual and postero-lingual roots. These specimens can be distinguished from *A. speciosus* by the root morphology only, because such a fused root is more elongated in cross section than the corresponding root of *A. speciosus*. A very short vestigial root is very rarely observed on the buccal side between the anterior and posterior roots (only in three specimens from Layer 1 of Locality 3 of Ube Kosan Quarry and Horizon N of Kannondo Cave Site; KUJC97163, 97241 and HUA-K00212).

M^2 ——

The outline and pattern are approximately coincident with those of *A. speciosus*. The anterostyle is well-developed and nearly as large as the enterostyle. The labial anterocone is more frequently found and more distinct than that of *A. speciosus*. It usually forms a low but distinct tubercle on the antero-buccal face of the protocone. In some cases, however, it is represented only by a short cingulum as in many specimens of *A. speciosus*. The variation in the degree of the development of this cusp is discussed in the next section.

In early stages of wear, the anterior and posterior chevrons are united on their buccal sides, because the paracone and metacone are closely arranged. On the other hand, the isthmus between the enterostyle and posterostyle is considerably broader and deeper. In worn teeth, however, this isthmus disappears, and the ring formed by the anterior and posterior chevrons is completed.

The ridge extending from the antero-buccal face of the hypocone reaches the metacone. The position of this ridge is somewhat more anterior than that of *A. speciosus*. In contrast with M^2 of *A. speciosus*, the posterior cingulum is always well-developed, and shapes an elongated ellipse in occlusal view. It is attached on the postero-buccal face of the hypocone, and extends nearly parallel to the ridge between the hypocone and metacone. The valley between the ridge and posterior cingulum is as distinct as in M^1. As the wear is advanced, the occlusal surface of the posterior cingulum readily connects with that of the metacone. As already mentioned, this character is also observable in M^1 of the present fossils, but never observed in M^1 and M^2 of *A. speciosus*. The metacone is generally smaller than the posterostyle and sometimes represented as a slight swelling of the ridge connecting the paracone with the posterior cingulum. The posterostyle is well developed.

Exceptionally, the above-mentioned ridge which directly connects the hypocone with the metacone is absent only in four specimens from Locality 4 of Ube Kosan Quarry (ASM 701565, 701581, 701586 and 701597). In such a case, the molar pattern is identical with "*giliacus* type" (Fig. 160).

M^2 always carries four roots. Their cross sections are round except the postero-lingual root which has a somewhat elongated cross section. These roots have nearly the same size, but the antero-lingual or postero-buccal roots are sometimes larger. In other cases, the postero-buccal root is somewhat smaller than the others.

M^3 ——

M^3 has a round occlusal outline. The general structure of the crown is similar to that of *A. speciosus*, but easily distinguishable from the latter by the disposition of the laminas and other characters.

The crown is composed of two transverse laminas (anterior and posterior laminas) and one well-developed antero-lingual cusp (anterostyle) as in *A. speciosus.* These laminas connect with each other on the buccal side. The anterostyle is round in occlusal view, and distinctly separated from the anterior lamina by a deep valley, so that its occlusal surface is not confluent with that of the anterior lamina even in considerably worn teeth. An accessory cusp is rarely found at the antero-buccal corner of the crown (labial anterocone). The frequency of the appearance of this cusp is described in the next section.

The anterior and posterior laminas comprise two cusps respectively, but they are completely fused with each other even in early stages of wear. Consequently, it can be said that the lophodont condition is more advanced in M^3 of the present fossils than in that of *A. speciosus.* These two laminas are set transverse to the long axis of the crown, and are arranged approximately parallel to each other. The occlusal surface of the buccal half of the anterior lamina is gradually expanded anteriorly by the wear of the crown, but its feature is distinguishable from that of *A. speciosus* where the whole part of the anterior lamina is obliquely disposed.

The valley between these two laminas is very deep and rather slender, but somewhat tapers at its buccal or both ends. It extends transversely in relation to the disposition of the laminas, but not so obliquely as in *A. speciosus.* In worn teeth, it becomes a closed slit-like pit in contrast with a rounded pit in the case of *A. speciosus.*

M^3 generally has three roots, namely antero-lingual, antero-buccal and posterior roots. They are round in cross section. The antero-lingual and antero-buccal roots have about the same size, and are very rarely fused into one root. The cross section of such a fused root is a transversely elongated ellipse in shape. The posterior root is more or less larger than the anterior roots, and remarkably extends postero-dorsally.

Mandible ——

The morphological characters of the mandible are generally identical with the above-mentioned generic characters. However the mandible is remarkably smaller and more delicately built than that of *A. speciosus.* The diastema is relatively shorter than that of *A. speciosus.* The alveolar pattern is identical with that of *A. speciosus* (Figs. 172, 180). The number of the alveolar pits is almost always six, corresponding to the total number of the roots of the molars.

M_1 ——

The occlusal outline and tooth pattern of M_1 are nearly identical with those of *A. speciosus.* The medial anteroconid is isolated from the lingual and labial anteroconids in slightly worn teeth, but easily connects with the last two cusps at their juncture, or the antero-buccal part of the lingual anteroconid, by the advance of wear. The posterior spur of the lingual anteroconid is sometimes present, but it is small and indistinct. The anterior and medial mures are absent.

The number of the buccal accessory cusps is generally two to four as in *A. speciosus.* These cusps show a wide range of variation in number and the degree of development. They are morphologically analysed in the next section. The low ridge ex-

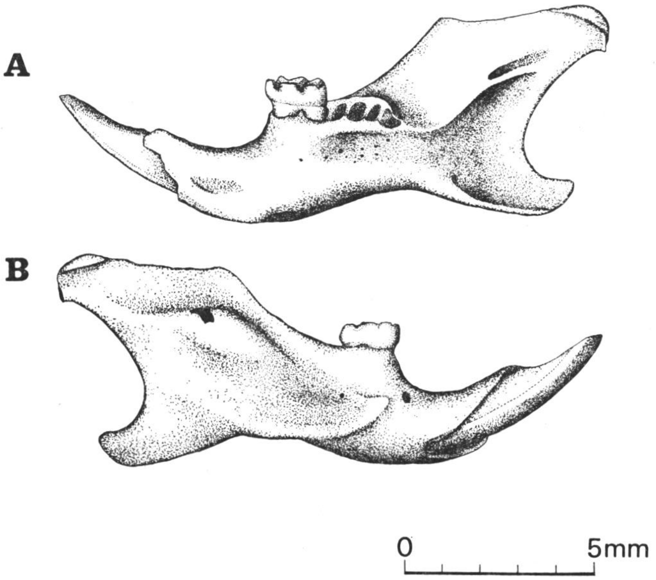


Fig. 182. *Apodemus argenteus*. Right mandible with I and M_1 from Layer 3 of Locality 3 of Ube Kosan Quarry (KUJC97281). A, lingual view; B, buccal view.

tending from C1 to C3 is absent or indistinct. Consequently the incision between C1 and C3 is generally deeper and more distinct than that of *A. speciosus*. Because the valley between C1 and the hypoconid is deep, these cusps are separated from each other until later stages of wear.

A lingual accessory cusp is very rarely found. Only in two specimens from Layer 18 of Locality 3 of Ube Kosan Quarry (KUJC97786 and 97790), it is observed at the lingual entrance of the valley between the anterior and middle chevrons. On the other hand, only in one specimen from Locality 4 of Ube Kosan Quarry (ASM 701680), it is present at the lingual entrance of the valley between the middle and posterior chevrons.

Almost all the specimens have two roots. The cross section of the anterior root is round or sometimes elliptical. This root is not so strong as that of *A. speciosus*. The posterior root has an elliptical cross section elongated transversely. In addition to these main roots, a small vestigial root is rarely observed on the median line of the tooth between the main roots. Exceptionally, two vestigial roots are found only in one specimen from Layer 3 of Locality 3 of Ube Kosan Quarry (KUJC97697).

M_2——

The crown comprises two chevrons and two isolated cusps. Their shapes and disposition as well as the outline of the crown are approximately identical with those of M_2 of *A. speciosus*. But some differences from the latter species are also observable in the morphology of the accessory cusps and cingulums on the buccal side, although there are no significant differences between the present fossils and *A. speciosus* in the corresponding part of M_1.

These cusps and cingulums are generally less developed than those of *A. speciosus.* In many specimens, they are completely absent. If they are present, the cusps are one or two in number, and the cingulums are weak and incontinuous. In contrast with *A. speciosus,* the accessory cusp on the buccal face of the hypoconid (possibly C1) is sometimes absent, and moreover C2 at the buccal entrance of the valley between the anterior and posterior chevrons is mostly lacking. Therefore this valley generally opens buccally without any obstacles. C3 is sometimes observed immediately posterior to the labial anteroconid. The variability of these cusps and cingulums is discussed in detail in the next section.

M_2 always have only two roots. Their morphology is identical with that of *A. speciosus.*

M_3——

The crown has a sub-triangular outline with round corners or a sub-round outline with a straight front margin. Its pattern comprising the anterior chevron and entoconid is similar to that of *A. speciosus,* but some differences from the latter species can be found by detailed observations.

The protoconid and metaconid are arranged approximately in the same transverse line. The former is nearly as large as the latter. The entoconid is much larger than these cusps, and separated from them by a deep transverse valley. It has a collumnar shape elongated laterally, so that its transverse width comes near to that of the anterior chevron. In slightly worn teeth, the occlusal surface of the entoconid is shaped like a lamina, which is set parallel to the occlusal surface of the anterior chevron. As the wear is advanced, it expands antero-posteriorly to be an elliptical shape elongated transversely. In considerably worn teeth, it finally shows an oval shape. Taking such an ontogenetic change into consideration, it can be said that the occlusal surface of the entoconid of the present fossils is generally slenderer than that of *A. speciosus.* The posterior face of the entoconid is almost always smooth as that of *A. speciosus,* but only in one specimen from Layer 3 of Locality 3 of Ube Kosan Quarry (KUJC98018), a very shallow longitudinal groove is observed on the midline of this face. On the other hand, a weak cingulum is also found on this face only in four specimens (ASM 701968 and 701986 from Locality 4 of Ube Kosan Quarry; KUJC97969 from Layer 1 of Locality 3 of Ube Kosan Quarry; ASM 703366 from Layer 1 of Tanuki-ana Cave).

The labial anteroconid is very rarely found on the antero-buccal face of the protoconid (only in five specimens out of hundreds of the fossil materials; ASM 701980 and 701983 from Locality 4 of Ube Kosan Quarry; KUJC97996 from Layer 3 of Locality 3 of the same quarry; ASM 703357 and 703366 from Layers 2 and 1 of Tanuki-ana Cave). If present, it is weak, and is sometimes represented only as a cingulum.

Table 96. Morphological variation on the anterior face of M^1 of *Apodemus argenteus*. The absence or presence of the prestyle and/or precingulum is analysed. The number of the specimens belonging to each morphotype is tabulated. The illustration of the morphotypes is given in Table 82.

LOCALITY	PRESTYLE(*ps*) AND PRECINGULUM(*prc*)				TOTAL
	ps and *prc* absent	*ps* present	*prc* present	*ps* and *prc* present	
RECENT MATERIALS					
Myogata	11	0	0	0	11
Gujohachiman	23	2	0	0	25
Mikawa Heights	30	0	0	0	30
Akiyoshi	8	0	0	0	8
HOLOCENE					
Tanuki-ana Cave					
Layer 1	2	0	0	0	2
Layer 2	20	1	0	0	21
Layers 2 to 3	3	0	0	0	3
Layer 3	7	0	0	0	7
Layer 4	30	0	0	0	30
Domen Site (Horizon V)	3	1	0	0	4
LATE PLEISTOCENE					
Kannondo Cave Site					
Horizon M (upper)	5	0	0	0	5
Horizon M (lower)	4	0	0	0	4
Horizon N	4	0	0	0	4
Horizon O (upper)	19	0	0	0	19
Horizon O (lower)	5	0	0	0	5
Horizon P	4	0	0	0	4
Sugi-ana Cave	9	0	0	0	9
MIDDLE PLEISTOCENE					
Loc.1 of Ube Kosan Quarry (total)	8	0	0	0	8
Loc.3 of Ube Kosan Quarry					
Layer 18	26	0	0	0	26
Layer 17	14	0	0	0	14
Layer 3	39	1	0	0	40
Layer 1	37	0	0	0	37
Loc.4 of Ube Kosan Quarry	71	8	0	0	79

M_3 always has two roots, namely anterior and posterior roots. Their shapes and relative sizes are identical with those of *A. speciosus*.

Morphological analyses of the molars

The representative fossil specimens from the Holocene, Late Pleistocene and Middle Pleistocene localities are examined for the morphological analyses of the molars. The recent specimens of *A. argenteus* from four localities in central Honshu are also analysed for comparison. The same analytical methods as used for *A.*

Table 97. Variation of the posterior spurs of the anterostyle and labial anterocone in M^1 of *Apodemus argenteus*. Four morphotypes are recognized as in M^1 of *A. speciosus* (see Table 83). The number of the specimens belonging to each morphotype is tabulated.

	POSTERIOR SPURS OF ANTEROSTYLE (*as*) AND LABIAL ANTEROCONE (*la*)				
LOCALITY	absent	present in *as*	present in *la*	present in *as* and *la*	TOTAL
RECENT MATERIALS					
Myogata	2	1	5	3	11
Gujohachiman	0	0	17	8	25
Mikawa Heights	0	0	18	12	30
Akiyoshi	3	0	5	1	9
HOLOCENE					
Tanuki-ana Cave					
Layer 1	0	0	1	0	1
Layer 2	7	0	10	3	20
Layers 2 to 3	1	0	3	0	4
Layer 3	0	0	5	2	7
Layer 4	13	0	16	5	34
Domen Site (Horizon V)	2	0	2	0	4
LATE PLEISTOCENE					
Kannondo Cave Site					
Horizon M (upper)	2	0	2	1	5
Horizon M (lower)	3	0	2	0	5
Horizon N	2	0	2	0	4
Horizon O (upper)	4	0	10	6	20
Horizon O (lower)	1	1	2	1	5
Horizon P	0	1	3	1	5
Sugi-ana Cave	5	0	3	1	9
MIDDLE PLEISTOCENE					
Loc.1 of Ube Kosan Quarry (total)	1	0	3	4	8
Loc.3 of Ube Kosan Quarry					
Layer 18	1	0	23	2	26
Layer 17	1	0	11	1	13
Layer 3	6	0	27	7	40
Layer 1	4	1	25	8	38
Loc.4 of Ube Kosan Quarry	15	2	38	21	76

speciosus are adopted here. The definitions of each morphotype are entirely identical with those of *A. speciosus* described in the preceding section (pp.33–46). Because the results of the present analyses indicate that there are no essential differences in the examined characters between the recent *A. argenteus* and present fossils, their identification as *A. argenteus* is also warranted.

Prestyle and precingulum of M^1 ——

The frequencies of the appearances of the prestyle and precingulum on the anterior face of M^1 are analysed. The results of the analysis are given in Table 96

Table 98. Variation of the number of roots in M^1 of *Apodemus argenteus*. The number of roots ranges from three to five. In the specimens with three roots, the posterior root exhibits the characteristic feature which indicates the fusion of two roots as figured below. The number of the specimens belonging to each morphotype is tabulated.

LOCALITY	NUMBER OF ROOTS			TOTAL
	3 	4 	5 	
HOLOCENE				
Tanuki-ana Cave				
Layer 1	0	1	0	1
Layer 2	0	14	0	14
Layers 2 to 3	0	2	0	2
Layer 3	0	3	1	4
Layer 4	0	20	4	24
LATE PLEISTOCENE				
Kannondo Cave Site				
Horizon M (upper)	0	5	0	5
Horizon M (lower)	0	4	0	4
Horizon N	0	3	0	3
Horizon O (upper)	0	16	2	18
Horizon O (lower)	0	4	1	5
Horizon P	0	3	2	5
Sugi-ana Cave	0	6	0	6
MIDDLE PLEISTOCENE				
Loc.3 of Ube Kosan Quarry				
Layer 18	0	5	1	6
Layer 17	0	2	0	2
Layer 3	1	9	0	10
Layer 1	1	15	3	19

and Fig. 183. These table and figure indicate that the precingulum is always absent from any population, but the prestyle is rarely found. The frequency of the appearance of the prestyle is generally low (0–2.7%), but exceptionally higher in the population of Locality 4 of Ube Kosan Quarry (10.1%). In comparison with *A. speciosus*, the appearances of these structures are remarkably rarer.

Posterior spurs of the anterostyle and labial anterocone of M^1 ——

The frequencies of the appearances of the posterior spurs of the anterostyle and labial anterocone are analysed (Table 97 and Fig. 183). Both of the spurs are absent from 6.7 to 31.8% of the total specimens. Such frequencies are much lower than those in *A. speciosus* (48.9–78.4%). Consequently it can be said that both or one of these spurs appear more frequently than in *A. speciosus*.

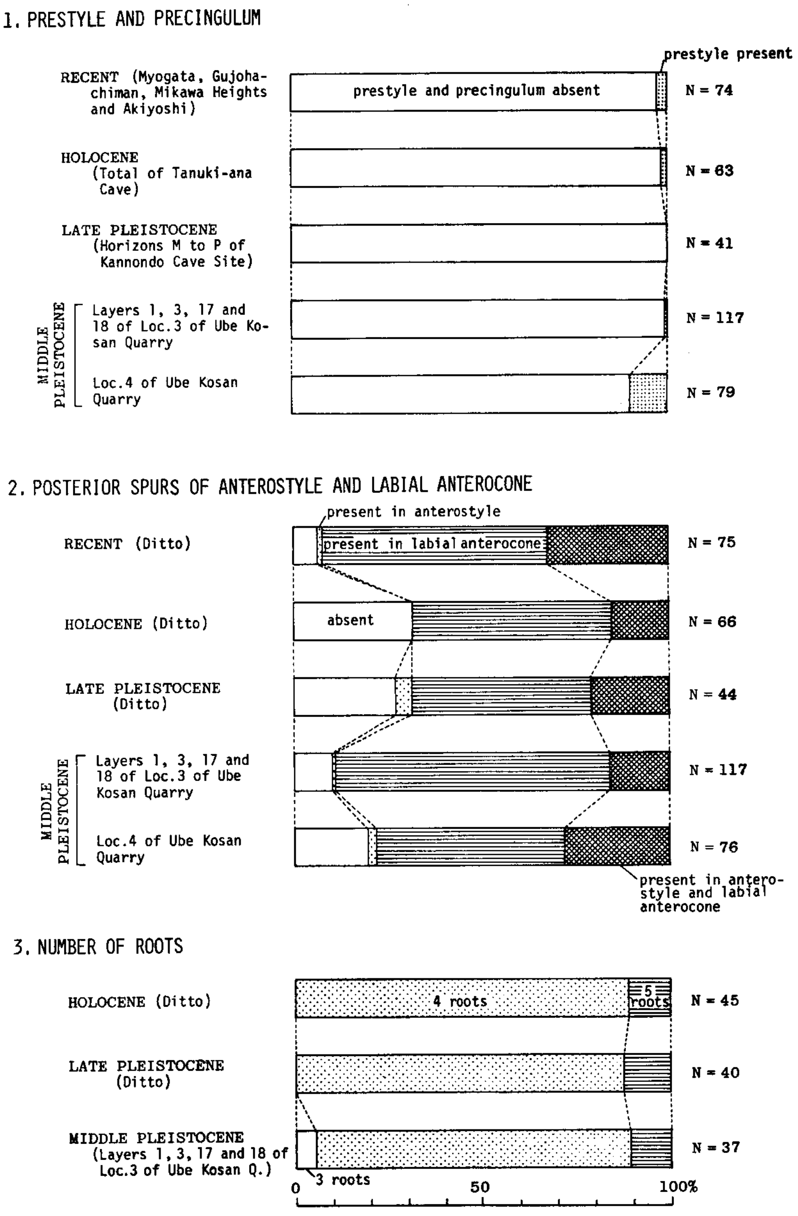


Fig. 183. Morphological variation in M^1 of *Apodemus argenteus*. The frequencies of each morphotype are illustrated. The data given in Tables 96, 97 and 98 are used. 1, variation of the prestyle and precingulum; 2, variation in the posterior spurs of the anterostyle and labial anterocone; 3, variation in the number of roots. N, number of specimens.

Table 99. Morphological variation on the anterior face of M^2 of *Apodemus argenteus*. The degree of the development of the labial anterocone is analysed. Each morphotype corresponds to that in M^2 of *A. speciosus* illustrated in Table 85. The number of the specimens belonging to each morphotype is tabulated.

LOCALITY	LABIAL ANTEROCONE				
	completely absent	represented as a cingulum	moderately developed	well developed	TOTAL
RECENT MATERIALS					
Myogata	0	3	5	3	11
Gujohachiman	0	0	12	13	25
Mikawa Heights	1	3	13	12	29
Akiyoshi	0	3	5	1	9
HOLOCENE					
Tanuki-ana Cave					
Layer 2	0	1	4	1	6
Layers 2 to 3	0	0	2	0	2
Layer 3	0	1	2	1	4
Layer 4	0	0	7	5	12
LATE PLEISTOCENE					
Kannondo Cave Site					
Horizon M (upper)	0	0	2	0	2
Horizon M (lower)	0	0	2	1	3
Horizon N	0	0	2	0	2
Horizon O (upper)	0	0	2	1	3
Horizon O (lower)	0	1	3	1	5
Sugi-ana Cave	0	2	4	2	8
MIDDLE PLEISTOCENE					
Loc.1 of Ube Kosan Quarry (total)	0	0	1	0	1
Loc.3 of Ube Kosan Quarry					
Layer 18	0	1	9	1	11
Layer 17	0	0	3	0	3
Layer 3	2	4	18	1	25
Layer 1	1	6	22	2	31
Loc.4 of Ube Kosan Quarry	2	6	54	12	74

The posterior spur of the anterostyle is present in 0 to 4.6% of the examined specimens, while that of the labial anterocone is present in 50.0–73.5% of the specimens. The frequency of the latter is much higher than in *A. speciosus* (14.2–23.9%). In 15.2 to 32.0% of the examined specimens, the posterior spurs are observable both in the anterostyle and labial anterocone. Because the frequencies of each morphotype fluctuate irregularly from population to population, the tendency of their temporal changes is not obvious.

Number of roots of M^1 ——

As concerns the number of roots, three morphotypes are recognized; namely

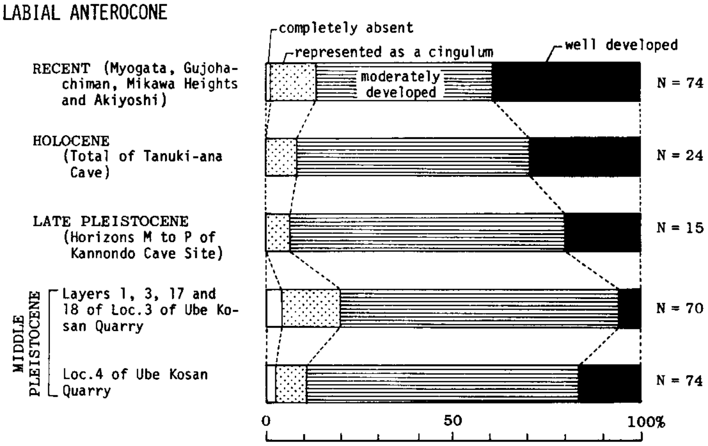


Fig. 184. Variation in the labial anterocone of M² of *Apodemus argenteus*. The frequencies of each morphotype are illustrated. The data given in Table 99 are used. N, number of specimens.

three-rooted, four-rooted and five-rooted types as illustrated in Table 98. Three populations of different geological ages are exclusively examined.

The three-rooted type is rare (0–5.4%) and appears only in the Middle Pleistocene population. The four-rooted type is most abundantly found in every population (83.8 to 88.9%). The frequency of the five-rooted type is relatively low (10.8 to 12.5%). The frequencies of each morphotype are rather stable among the fossil populations, so that their temporal changes are hardly observed.

Labial anterocone of M^2 ——

The degree of the development of the labial anterocone is analysed by means of the recognition of the four morphotypes as in *A. speciosus*. The results of the analysis are given in Table 99 and Fig. 184.

The frequencies of the "completely absent" type are remarkably low (0–4.3%). Those of the type of "labial anterocone represented as a cingulum" are slightly higher (6.7–15.7%). The "moderately developed" type is most frequently found in every populatian (47.3–74.3%), while the frequencies of the "well-developed" type are much lower (5.7–39.2%). If the "moderately developed" type and "well-developed" type are combined, the temporal changes of the frequencies of each morphotype are rather slight. In comparison with *A. speciosus*, it can be stated that the labial anterocone is much better developed in the present fossil populations and the recent *A. argenteus*.

Accessory cusp (labial anterocone) of M^3 ——

The presence or absence of the accessory cusp on the antero-buccal face of the protocone is examined (Table 100). This cusp is absent from all the fossil populations, but rarely found in the populations of the living *A. argenteus* (10.9%).

Table 100. Morphological variation in M^3 of *Apodemus argenteus*. The specimens are classified into two morphotypes by the absence or presence of the accessory cusp. The number of the specimens belonging to each morphotype is tabulated.

	ACCESSORY CUSP		
LOCALITY	absent 	present 	TOTAL
RECENT MATERIALS			
Myogata	8	2	10
Gujohachiman	22	1	23
Mikawa Heights	19	4	23
Akiyoshi	8	0	8
HOLOCENE			
Tanuki-ana Cave			
Layer 2	1	0	1
Layers 2 to 3	1	0	1
Layer 4	3	0	3
LATE PLEISTOCENE			
Kannondo Cave Site			
Horizon M (upper)	2	0	2
Horizon N	1	0	1
Horizon O (lower)	2	0	2
Sugi-ana Cave	3	0	3
MIDDLE PLEISTOCENE			
Loc.3 of Ube Kosan Quarry			
Layer 18	3	0	3
Layer 3	13	0	13
Layer 1	10	0	10
Loc.4 of Ube Kosan Quarry	24	0	24

Buccal accessory cusps of M_1 ——

In order to analyse the variation of the buccal accessory cusps, the six morphotypes (morphotypes A to F) are recognized as in *A. speciosus* (Fig. 178). The following three populations with different geological ages are examined:

1. Recent *A. argenteus* (N=65); combined materials from Myogata, Gujohachiman and Mikawa Heights.
2. Late Pleistocene population (N=39); combined materials from Horizons M, N and O of Kannondo Cave Site.
3. Middle Pleistocene population (N=117); combined materials from Layers 1, 3, 17 and 18 of Locality 3 of Ube Kosan Quarry.

The morphotype C is most abundantly found in all the populations (56.4–61.5%). The frequency of the morphotype D fluctuates from 12.3% (in the Late and Middle Pleistocene populations) to 35.4% (in the recent population). Those of the morphotypes E and F are much lower (1.7–10.3% and 1.7–7.7% respectively). The morphotype B is absent from the recent and Late Pleistocene populations, but rarely found in the Middle Pleistocene population (6.0%). On the other hand, the morphotype A is absent only from the recent population, but gradually increases from the Late Pleistocene population (7.7%) to the Middle Pleistocene population (18.0%).

The tendency of the temporal change is not so obvious in the frequency of each morphotype. As regards the interspecific differences, TOKUDA (1968) stated that the buccal accessory cusps were better developed in *A. argenteus* than in *A. speciosus*. But as far as the present examined materials are concerned, such a difference is invisible.

Buccal accessory cusps of M_2 ——

The variation of the buccal accessory cusps is analysed by recognizing the eight morphotypes as in *A. speciosus* (morphotypes A to H; Fig. 179). The following three populations with different geological ages are examined:

1. Recent *A. argenteus* (N=63); combined materials from Myogata, Gujohachiman and Mikawa Heights.
2. Late Pleistocene population (N=20); combined materials from Horizons M and N of Kannondo Cave Site.
3. Middle Pleistocene population (N=72); combined materials from Layers 1, 3, 17 and 18 of Locality 3 of Ube Kosan Quarry.

The frequencies of the morphotypes A, C, D and E are relatively higher than those of the others. The morphotype A increases from the recent population (15.9%) to the Middle Pleistocene population (56.9%), whereas the morphotype E decreases from the former (34.9%) to the latter (12.5%). The frequencies of the morphotypes C and D are rather constant among the different populations (10.0–18.1 and 22.2–30.0% respectively). On the other hand, the morphotypes B, F and G are rather rarely found (2.8–10.0, 0–1.6 and 0–5.0% respectively), and the morphotype H is absent from all the populations.

As concerns the temporal changes, in general, the combined frequency of the simpler morphotypes (A, B and C) gradually increases from the recent to Middle Pleistocene populations, but that of the more complicate morphotypes (D, E, F and G) gradually decreases. In comparison with the results of the same analysis in *A. speciosus*, the simpler morphotypes appear more frequently in all the populations. Consequently the degree of the development of the accessory cusps of M_2 is different between *A. argenteus* and *A. speciosus* in contrast with that of M_1 where no significant interspecific differences are observed.

Measurements

The measurements of the representative mandibles are given in Table 101. Those of the molars are also given in Tables 102–107. The temporal change in molar size will be discussed in the separate paper as in *A. speciosus*.

Comparisons

In order to ascertain the identification of the fossil materials as *A. argenteus*, the

Table 101. Measurements of the mandibles of *Apodemus argenteus* in mm. The numbers on the left side correspond to those in Fig. 72.

	Kannondo Site (Holocene)			Kumai-shi-do Cave, F_3	Kannondo Site (Late Pleistocene)			Sugi-ana Cave			Locality 3 of Ube Kosan Quarry Layer 3			Ikumo Quarry
	Horizon J	Horizon K			Horizon M		Horizon N							
	HUA-K 04104	HUA-K 04100	HUA-K 04101	YKS 02148	HUA-K 00031	HUA-K 00047	HUA-K 00249	KUJC 100474	KUJC 100477	KUJC 100509	KUJC 97278	KUJC 97281	KUJC 97282	ASM 700009
2. Total length of the mandible (id to the condyle)	13.44 ±	–	–	13.01 ±	–	–	–	–	–	–	–	–	–	–
3. Length from the tip of the incisor to the condyle	14.86 ±	–	–	–	–	–	–	15.35	–	–	–	–	–	–
4. Length of the horizontal ramus	7.42	–	–	6.95	–	–	6.87	–	–	6.84	7.18	–	–	6.45
5. Length of the diastema	4.06	3.99	–	3.47	–	–	3.64	–	–	3.50	3.75	–	–	3.36 ±
6. Length of the ascending ramus (the posterior border of M_3 to the condyle)	6.29 ±	–	6.16 ±	6.30 ±	–	–	–	6.34	–	–	–	–	–	–
8. Height of the ascending ramus (gov to the highest point of the condyle)	–	–	–	–	–	–	–	–	–	–	–	5.61	–	–
11. Length of the mandibular incision	–	–	–	–	–	–	–	3.81	–	–	–	–	–	–
12. Height of the horizontal ramus at M_1	2.65	2.69	2.45	–	2.47	2.53	2.58	2.57 ±	2.35	–	2.54	2.59	2.77	2.46
13. Height of the horizontal ramus at M_3	1.94	–	1.95	2.06	1.92	1.87	1.87	2.38	1.99	1.65	1.99	–	2.17	1.99
14. Maximum thickness of the horizontal ramus	1.62	1.50	1.51	–	1.54	1.43	1.72	1.57	1.60	1.38	1.66	1.70	1.61	1.49
15. Length of the molar row (M_1 to M_3) at the crowns	3.75	–	3.44	–	3.65	–	–	3.59	3.50	–	–	–	3.04	–
16. Ditto at the alveoli	3.52	–	3.23	3.63	3.51	3.44	3.41	3.45	3.43	3.45	3.52	–	3.12	3.18 ±
17. Length of the molar row (M_1 to M_2) at the crowns	2.86	2.55	2.59	–	2.74	–	–	2.68	2.68	–	2.65	–	2.32	–
18. Ditto at the alveoli	2.53	2.25	2.27	2.60	2.52	2.45	2.37	2.27	2.52	2.47	2.56	2.44	2.26	2.28 ±

Table 102. Measurements of M^1 of *Apodemus argenteus*. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	4	1.71	1.77	1.79	–	4	1.01	1.06	1.12	–
Nopporo	2	1.65	1.69	1.73	–	2	1.02	1.03	1.05	–
Noboribetsu	1	–	1.78	–	–	1	–	1.11	–	–
Otaki	1	–	1.77	–	–	1	–	1.11	–	–
HONSHU										
Karumai	1	–	1.73	–	–	1	–	1.17	–	–
Miyako	1	–	1.92	–	–	1	–	1.14	–	–
Sugaya	1	–	1.87	–	–	1	–	1.18	–	–
Mt.Takao	4	1.73	1.75	1.76	–	4	1.06	1.10	1.14	–
Myogata	12	1.62	1.77	1.87	0.07	12	1.00	1.10	1.16	0.05
Gujohachiman	26	1.50	1.76	1.89	0.08	26	0.97	1.09	1.16	0.04
Mikawa Heights	30	1.64	1.79	1.88	0.07	30	1.05	1.14	1.26	0.05
Tokuyama	1	–	1.70	–	–	1	–	1.09	–	–
Akiyoshi	9	1.64	1.73	1.85	0.07	9	1.01	1.06	1.12	0.03
HOLOCENE										
Husen-ana Cave	3	1.65	1.72	1.78	–	3	1.06	1.10	1.14	–
Tanuki-ana Cave (Layer 2)	1	–	1.76	–	–	1	–	1.10	–	–
Domen Site (Horizon V)	4	1.75	1.79	1.84	–	4	1.04	1.10	1.17	–
Kannondo Cave Site										
Horizon unknown	1	–	1.84	–	–	1	–	1.13	–	–
Horizon I	2	1.71	1.78	1.85	–	2	1.13	1.15	1.17	–
LATE PLEISTOCENE										
Kumaishi-do Cave										
F_1, F_2 and F_4	3	1.76	1.81	1.85	–	3	0.93	1.03	1.16	–
F_3	26	1.56	1.74	1.87	0.10	26	0.89	1.07	1.19	0.07
Kannondo Cave Site										
Horizon M (upper)	5	1.71	1.77	1.85	0.05	4	0.99	1.07	1.12	–
Horizon M (lower)	4	1.66	1.68	1.71	–	5	1.01	1.05	1.09	0.03
Horizon N	4	1.58	1.70	1.83	–	4	1.02	1.04	1.06	–
Horizon O (upper)	7	1.65	1.78	1.94	0.08	7	1.01	1.10	1.17	0.05
Horizon O (lower)	5	1.61	1.78	1.92	0.11	5	1.05	1.14	1.18	0.05
Horizon P	5	1.62	1.73	1.76	0.06	5	1.02	1.09	1.15	0.05
Yage Quarry (Site 4)	1	–	1.80	–	–	1	–	1.07	–	–
Sugi-ana Cave	8	1.64	1.78	1.89	0.07	9	0.96	1.09	1.14	0.05
Aisawa Quarry	3	1.71	1.75	1.77	–	3	1.07	1.09	1.10	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	5	1.75	1.80	1.88	0.04	5	1.05	1.08	1.15	0.04
Layer 3	3	1.71	1.80	1.90	–	3	1.05	1.11	1.19	–
Loc.3 of Ube Kosan Quarry										
Layer 18	24	1.62	1.80	1.97	0.09	27	0.98	1.07	1.13	0.04
Layer 17	13	1.71	1.82	1.96	0.08	14	1.03	1.09	1.13	0.04
Layer 3	40	1.64	1.80	1.92	0.07	40	0.98	1.08	1.14	0.04
Layer 1	38	1.63	1.78	1.92	0.07	38	0.98	1.08	1.17	0.04
Loc.4 of Ube Kosan Quarry	75	1.62	1.78	1.95	0.07	81	0.95	1.08	1.20	0.04

extensive comparisons with the living and fossil species of *Apodemus* are carried out in this section.

Comparisons with the East Asiatic living species of Apodemus ——

In accordance with CORBET (1978), the five species of *Apodemus* are known from East Asia, as listed in the section of *A. speciosus* (p. 47). *A. agrarius* is somewhat larger than the present fossil materials. In this species, the posterior cingulums of M^1 and M^2 are generally absent or poorly developed, although they are remarkably developed in the present fossils. In addition to these characters, the occlusal pattern of M^3 is also different between them. *A. peninsulae* is easily distinguishable from the present fossils by the following characters: (1) the size is somewhat larger;

Table 103. Measurements of M^2 of *Apodemus argenteus*. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	4	1.09	1.12	1.14	–	4	0.94	0.98	1.04	–
Nopporo	2	1.14	1.14	1.15	–	2	0.90	0.97	1.03	–
Noboribetsu	1	–	1.12	–	–	1	–	1.04	–	–
Otaki	1	–	1.20	–	–	1	–	1.02	–	–
HONSHU										
Karumai	1	–	1.12	–	–	1	–	1.07	–	–
Miyako	1	–	1.21	–	–	1	–	1.05	–	–
Sugaya	1	–	1.18	–	–	1	–	1.04	–	–
Mt.Takao	4	1.08	1.10	1.13	–	4	1.01	1.04	1.08	–
Myogata	12	1.04	1.12	1.17	0.06	12	0.93	1.03	1.08	0.04
Gujohachiman	26	0.95	1.11	1.21	0.07	26	0.92	1.00	1.08	0.04
Mikawa Heights	30	1.09	1.17	1.23	0.04	30	0.94	1.04	1.12	0.03
Tokuyama	1	–	1.12	–	–	1	–	1.00	–	–
Akiyoshi	9	1.02	1.10	1.16	0.05	9	0.96	1.00	1.04	0.03
HOLOCENE										
Husen-ana Cave	1	–	1.06	–	–	1	–	0.96	–	–
Tanuki-ana Cave (Layer 2)	2	1.12	1.12	1.12	–	2	1.00	1.01	1.02	–
Kannondo Site (Horizon I)	1	–	1.18	–	–	1	–	1.04	–	–
LATE PLEISTOCENE										
Kumaishi-do Cave										
F_1, F_2 and F_4	1	–	1.14	–	–	1	–	1.06	–	–
F_3	14	1.04	1.13	1.23	0.06	14	0.88	0.99	1.11	0.06
Kannondo Cave Site										
Horizon M (upper)	2	1.06	1.09	1.11	–	2	0.95	0.96	0.97	–
Horizon M (lower)	3	1.00	1.15	1.28	–	4	0.79	0.95	1.09	–
Horizon N	2	1.02	1.06	1.10	–	2	0.98	0.98	0.98	–
Horizon O (upper)	2	1.04	1.04	1.04	–	2	0.97	0.99	1.01	–
Horizon O (lower)	5	1.05	1.16	1.24	0.07	5	0.93	1.00	1.05	0.05
Sugi-ana Cave	8	1.06	1.16	1.22	0.06	7	0.91	0.99	1.04	0.04
Loc.2 of Ube Kosan Quarry	5	0.99	1.12	1.18	0.07	5	0.91	0.97	1.02	0.03
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	1	–	1.26	–	–	1	–	0.97	–	–
Loc.3 of Ube Kosan Quarry										
Layer 18	11	1.03	1.14	1.20	0.05	9	0.88	0.98	1.05	0.04
Layer 17	3	1.14	1.19	1.22	–	3	0.95	0.98	1.03	–
Layer 3	25	1.05	1.17	1.33	0.06	24	0.85	0.98	1.03	0.04
Layer 1	32	0.96	1.14	1.31	0.07	32	0.88	0.98	1.09	0.04
Loc.4 of Ube Kosan Quarry	73	0.96	1.18	1.28	0.06	74	0.88	1.00	1.16	0.04

(2) M^1 and M^2 are three-rooted instead of four; (3) the direct connection between the hypocone and metacone is not formed in M^1 and M^2, but the former cusp connects with the latter through the posterior cingulum (namely "*giliacus* type"). *A. draco* differs from the present fossils by the number of roots in M^1. *A. latronum* and *A. semotus* are discriminated from them by the larger sizes. Additionally, the following characters are also diagnostic: In *A. latronum*, the number of roots of M^1 is usually three. In *A. semotus*, the buccal accessory cusps and cingulums of M_1 and M_2 seem to be better developed.

Comparisons with other living species ——

The present fossils are compared with the four representative species of *Apodemus* such as *A. mystacinus*, *A. flavicollis*, *A. sylvaticus* and *A. microps* which are distributed outside East Asia. M^1 and M^2 of these species are almost always four-rooted as those of the present fossils.

Table 104. Measurements of M^3 of *Apodemus argenteus*. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	4	0.70	0.77	0.89	–	4	0.70	0.74	0.79	–
Nopporo	2	0.77	0.80	0.83	–	2	0.74	0.75	0.77	–
Noboribetsu	1	–	0.79	–	–	1	–	0.76	–	–
Otaki	1	–	0.74	–	–	1	–	0.77	–	–
HONSHU										
Karumai	1	–	0.82	–	–	1	–	0.73	–	–
Miyako	1	–	0.89	–	–	1	–	0.87	–	–
Sugaya	1	–	0.87	–	–	1	–	0.78	–	–
Mt.Takao	2	0.85	0.86	0.86	–	2	0.81	0.82	0.82	–
Myogata	12	0.72	0.80	0.88	0.05	12	0.72	0.80	0.87	0.04
Gujohachiman	25	0.70	0.82	0.89	0.05	25	0.70	0.78	0.87	0.04
Mikawa Heights	30	0.74	0.82	0.94	0.05	30	0.71	0.80	0.87	0.04
Tokuyama	1	–	0.82	–	–	1	–	0.84	–	–
Akiyoshi	9	0.79	0.81	0.83	0.02	9	0.76	0.81	0.87	0.04
LATE PLEISTOCENE										
Kumaishi-do Cave (F_3)	5	0.72	0.78	0.87	0.05	5	0.70	0.77	0.82	0.04
Kannondo Cave Site										
Horizon M (upper)	2	0.72	0.76	0.80	–	2	0.71	0.73	0.75	–
Horizon N	1	–	0.81	–	–	1	–	0.77	–	–
Horizon O (lower)	2	0.81	0.82	0.83	–	2	0.72	0.73	0.74	–
Horizon P	1	–	0.79	–	–	1	–	0.67	–	–
Sugi-ana Cave	3	0.75	0.83	0.87	–	3	0.71	0.79	0.83	–
MIDDLE PLEISTOCENE										
Loc.3 of Ube Kosan Quarry										
Layer 18	3	0.77	0.81	0.87	–	3	0.77	0.79	0.81	–
Layer 17	1	–	0.79	–	–	1	–	0.70	–	–
Layer 3	13	0.70	0.80	0.87	0.04	13	0.72	0.78	0.86	0.04
Layer 1	11	0.72	0.78	0.87	0.04	11	0.71	0.75	0.82	0.04
Loc.4 of Ube Kosan Quarry	24	0.74	0.81	0.89	0.05	24	0.75	0.80	0.88	0.03

Although the posterior cingulums of M^1 and M^2 of *A. mystacinus* are well developed as those of the present fossils, its M^3 and M_3 patterns are rather similar to those of *A. speciosus* or *A. peninsulae*, but different from those of the present fossils. Moreover *A. mystacinus* is much larger than the fossils. *A. flavicollis* differs from them in having larger size, the M^3 pattern of "*speciosus* type" or "*giliacus* type" and labial anteroconid in M_3. *A. sylvaticus* is also different from them in having somewhat larger size, relatively larger incisive foramina, less developed posterior cingulums of M^1 and M^2, and the M^3 pattern of "*speciosus* type" or "*giliacus* type."

The size of *A. microps* is nearly as large as the present fossils. Moreover the masseteric plates of *A. microps* are relatively narrow antero-posteriorly as those of the present fossils, although those of *A. mystacinus*, *A. flavicollis* and *A. sylvaticus* are broader. In spite of these similarities, the present fossils can be distinguished from *A. microps* by the degree of the development of the posterior cingulums of M^1 and M^2, and by the pattern of M^3.

Comparisons with the Chinese fossil Apodemus ——

In comparison with the Early Pleistocene "*A.* cf. *sylvaticus*" from Huaiyu and the Middle Pleistocene "*A. sylvaticus*" from Locality 1 of Choukoutien, the present fossils are easily discriminated from them by the sizes and patterns of the upper molars. Namely, in these Chinese fossils, the sizes are generally larger, and the posterior

Table 105. Measurements of M_1 of *Apodemus argenteus*. * MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	4	1.54	1.61	1.66	–	4	0.93	0.97	1.02	–
Nopporo	2	1.56	1.57	1.59	–	2	0.95	0.96	0.97	–
Noboribetsu	1	–	1.65	–	–	1	–	0.98	–	–
Otaki	1	–	1.58	–	–	1	–	1.00	–	–
HONSHU										
Karumai	1	–	1.61	–	–	1	–	0.98	–	–
Miyako	1	–	1.80	–	–	1	–	1.10	–	–
Sugaya	1	–	1.58	–	–	1	–	1.06	–	–
Mt.Takao	4	1.63	1.65	1.69	–	4	0.95	1.00	1.06	–
Myogata	12	1.48	1.62	1.70	0.06	12	0.89	1.00	1.09	0.05
Gujohachiman	26	1.40	1.60	1.82	0.09	26	0.90	0.99	1.07	0.05
Mikawa Heights	30	1.52	1.63	1.82	0.06	30	0.93	1.00	1.06	0.04
Tokuyama	1	–	1.58	–	–	1	–	0.93	–	–
Akiyoshi	9	1.44	1.56	1.63	0.07	9	0.94	0.98	1.03	0.03
HOLOCENE										
Husen-ana Cave	4	1.56	1.64	1.72	–	4	0.96	1.02	1.06	–
Tanuki-ana Cave (Layer 2)	5	1.53	1.66	1.75	0.08	5	0.92	1.02	1.08	0.06
Domen Site (Horizon V)	3	1.54	1.56	1.60	–	3	0.92	0.95	0.97	–
Kannondo Cave Site										
Horizon unknown	3	1.55	1.64	1.71	–	3	0.93	0.97	0.99	–
Horizon I	6	1.57	1.67	1.77	0.07	6	0.96	1.03	1.08	0.04
Horizon J	4	1.43	1.62	1.69	–	4	0.93	1.03	1.09	–
Horizon K	3	1.56	1.58	1.63	–	3	0.98	0.99	1.01	–
Suse Quarry (West Fissure)*	1	–	1.64	–	–	1	–	1.00	–	–
LATE PLEISTOCENE										
Suse Quarry (East Fissure)*	2	1.52	1.53	1.54	–	2	0.92	0.96	1.00	–
Kumaishi-do Cave										
F_1, F_2 and F_4	6	1.44	1.58	1.75	0.10	6	0.88	0.94	1.04	0.06
F_3	23	1.50	1.61	1.72	0.05	23	0.89	0.96	1.06	0.04
Kannondo Cave Site										
Horizon M (upper)	8	1.48	1.58	1.66	0.06	9	0.90	0.97	1.02	0.04
Horizon M (lower)	8	1.43	1.61	1.75	0.10	8	0.92	1.00	1.07	0.05
Horizon N	15	1.46	1.61	1.73	0.08	15	0.88	0.96	1.03	0.05
Horizon O (upper)	11	1.55	1.62	1.71	0.05	11	0.90	0.97	1.03	0.03
Horizon O (lower)	10	1.40	1.58	1.73	0.09	11	0.95	0.99	1.03	0.03
Horizon P	2	1.54	1.59	1.64	–	2	0.88	0.91	0.94	–
Seiryukutsu Cave	2	1.63	1.64	1.64	–	2	1.01	1.02	1.04	–
Yage Quarry										
Site 2*	1	–	1.69	–	–	1	–	1.05	–	–
Site 4	1	–	1.51	–	–	1	–	0.92	–	–
Sugi-ana Cave	13	1.42	1.58	1.69	0.09	13	0.87	0.96	1.03	0.05
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 1	1	–	1.61	–	–	1	–	0.92	–	–
Layer 2	2	1.55	1.58	1.62	–	2	0.87	0.93	0.98	–
Loc.3 of Ube Kosan Quarry										
Layer 18	39	1.54	1.64	1.73	0.05	41	0.85	0.96	1.04	0.04
Layer 17	16	1.54	1.63	1.71	0.05	16	0.91	0.96	1.04	0.04
Layer 3	35	1.46	1.62	1.74	0.07	38	0.89	0.96	1.06	0.04
Layer 1	26	1.47	1.61	1.74	0.05	30	0.87	0.95	1.02	0.04
Loc.4 of Ube Kosan Quarry	103	1.45	1.62	1.75	0.07	106	0.85	0.97	1.03	0.04
Ikumo Quarry	1	–	1.57	–	–	1	–	0.92	–	–

cingulums of M^1 and M^2 are less developed. Moreover, their M^3 have different patterns from that of the present fossils. According to PEI (1936), M^1 of the Middle Pleistocene "*A. sylvaticus*" from Locality 3 of Choukoutien has four roots as the present fossils. However this form is larger, and has the patterns of the upper molars rather similar to *A. agrarius*. The other Middle Pleistocene records of *Apodemus* listed in Table 79 mostly show larger dimensions than the present fossils, although the available

Table 106. Measurements of M_2 of *Apodemus argenteus*. * MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	4	1.07	1.10	1.15	–	4	0.96	0.97	1.01	–
Nopporo	2	1.08	1.10	1.13	–	2	0.94	0.96	0.99	–
Noboribetsu	1	–	1.12	–	–	1	–	0.96	–	–
Otaki	1	–	1.10	–	–	1	–	0.96	–	–
HONSHU										
Karumai	1	–	1.18	–	–	1	–	0.97	–	–
Miyako	1	–	1.16	–	–	1	–	1.09	–	–
Sugaya	1	–	1.14	–	–	1	–	1.06	–	–
Mt.Takao	4	1.08	1.14	1.20	–	4	1.02	1.06	1.08	–
Myogata	12	1.08	1.14	1.20	0.04	12	0.95	1.03	1.12	0.04
Gujohachiman	26	1.02	1.13	1.21	0.05	26	0.92	1.00	1.08	0.04
Mikawa Heights	30	1.06	1.15	1.20	0.04	30	0.97	1.03	1.09	0.03
Tokuyama	1	–	1.05	–	–	1	–	0.98	–	–
Akiyoshi	9	1.06	1.12	1.19	0.05	9	0.93	0.98	1.02	0.03
HOLOCENE										
Husen-ana Cave	3	1.05	1.09	1.14	–	3	0.94	0.97	0.98	–
Tanuki-ana Cave (Layer 2)	4	1.07	1.13	1.18	–	4	1.00	1.03	1.04	–
Kannondo Cave Site										
Horizon unknown	3	1.09	1.15	1.23	–	3	0.99	1.05	1.15	–
Horizon I	6	1.16	1.26	1.33	0.06	6	1.03	1.08	1.14	0.04
Horizon J	3	1.14	1.20	1.25	–	3	1.03	1.05	1.07	–
Horizon K	3	1.06	1.10	1.17	–	3	0.99	1.02	1.05	–
LATE PLEISTOCENE										
Suse Quarry (East Fissure)*	1	–	1.13	–	–	1	–	1.02	–	–
Kumaishi-do Cave										
F_1, F_2 and F_4	2	0.97	1.06	1.16	–	2	0.97	1.01	1.04	–
F_3	20	1.00	1.10	1.20	0.05	20	0.92	0.99	1.04	0.03
Kannondo Cave Site										
Horizon M (upper)	7	1.05	1.14	1.19	0.04	8	0.89	1.01	1.09	0.05
Horizon M (lower)	4	1.10	1.15	1.20	–	4	0.94	1.01	1.06	–
Horizon N	9	1.09	1.14	1.17	0.03	9	0.90	0.99	1.04	0.04
Horizon O (upper)	1	–	1.11	–	–	1	–	1.03	–	–
Horizon O (lower)	8	1.06	1.13	1.21	0.06	8	0.96	1.01	1.05	0.02
Horizon P	2	1.03	1.09	1.15	–	2	0.90	0.94	0.99	–
Seiryukutsu Cave	2	1.09	1.11	1.12	–	2	0.99	1.01	1.02	–
Yage Quarry (Site 4)	1	–	1.12	–	–	1	–	0.99	–	–
Sugi-ana Cave	2	1.14	1.14	1.14	–	2	0.99	1.00	1.01	–
Aisawa Quarry	1	–	1.10	–	–	1	–	1.04	–	–
Loc.2 of Ube Kosan Quarry	2	1.00	1.01	1.03	–	2	0.91	0.93	0.95	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	3	1.10	1.13	1.14	–	3	0.94	0.97	1.00	–
Loc.3 of Ube Kosan Quarry										
Layer 18	19	1.04	1.10	1.18	0.04	19	0.91	0.99	1.08	0.05
Layer 17	8	1.05	1.10	1.18	0.05	8	0.95	1.00	1.04	0.03
Layer 3	34	0.95	1.13	1.22	0.05	34	0.90	0.99	1.11	0.04
Layer 1	25	0.99	1.13	1.18	0.04	25	0.91	0.99	1.09	0.05
Loc.4 of Ube Kosan Quarry	104	1.00	1.13	1.24	0.05	103	0.88	1.01	1.13	0.04
Ikumo Quarry	1	–	1.06	–	–	1	–	0.97	–	–

information to the present comparisons is insufficiently given in the literatures.

A. draco and *A. latronum* known from the Late Pleistocene sediments of Sanjiacun (QIU *et al.*, 1984) are distinguished from the present fossils by their larger sizes. They are also different from the latter in having poorly-developed posterior cingulums in M^1 and M^2. However the M^3 pattern of *A. draco* is similar to that of the present fossils, whereas that of *A. latronum* is comparable with "*giliacus* type." The other Late Pleistocene fossils of *Apodemus* are not described satisfactorily. Among them, M_2 of

Table 107. Measurements of M_3 of *Apodemus argenteus*. Abbreviations as in Table 38.

LOCALITY	LENGTH					WIDTH				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
HOKKAIDO										
Koshimizu	4	0.83	0.88	0.91	–	4	0.79	0.81	0.83	–
Nopporo	2	0.88	0.89	0.89	–	2	0.78	0.81	0.84	–
Noboribetsu	1	–	0.87	–	–	1	–	0.78	–	–
Otaki	1	–	0.90	–	–	1	–	0.83	–	–
HONSHU										
Karumai	1	–	0.93	–	–	1	–	0.84	–	–
Miyako	1	–	0.89	–	–	1	–	0.91	–	–
Sugaya	1	–	0.85	–	–	1	–	0.86	–	–
Mt.Takao	4	0.87	0.89	0.93	–	4	0.84	0.86	0.88	–
Myogata	12	0.89	0.94	0.99	0.04	12	0.80	0.87	0.92	0.04
Gujohachiman	26	0.80	0.94	1.02	0.06	26	0.78	0.85	0.90	0.04
Mikawa Heights	30	0.85	0.94	1.03	0.04	30	0.80	0.87	0.94	0.04
Tokuyama	1	–	0.87	–	–	1	–	0.84	–	–
Akiyoshi	9	0.86	0.94	1.00	0.04	9	0.80	0.85	0.91	0.03
HOLOCENE										
Kannondo Cave Site										
Horizon I	2	0.97	0.98	0.98	–	2	0.85	0.87	0.89	–
Horizon J	1	–	0.96	–	–	1	–	0.86	–	–
Horizon K	1	–	0.93	–	–	1	–	0.86	–	–
LATE PLEISTOCENE										
Kumaishi-do Cave										
F_3	7	0.81	0.89	1.01	0.07	7	0.77	0.81	0.84	0.02
Kannondo Cave Site										
Horizon M (upper)	3	0.94	0.95	0.96	–	3	0.85	0.88	0.90	–
Horizon N	1	–	0.98	–	–	1	–	0.85	–	–
Horizon P	3	0.87	0.92	1.00	–	3	0.77	0.84	0.91	–
Sugi-ana Cave	1	–	0.90	–	–	1	–	0.79	–	–
Loc.2 of Ube Kosan Quarry	1	–	0.90	–	–	1	–	0.78	–	–
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	1	–	0.90	–	–	1	–	0.83	–	–
Loc.3 of Ube Kosan Quarry										
Layer 18	9	0.92	0.96	1.04	0.04	9	0.81	0.85	0.89	0.02
Layer 17	3	0.90	0.91	0.92	–	3	0.80	0.83	0.86	–
Layer 3	30	0.84	0.94	1.06	0.06	29	0.75	0.84	0.92	0.04
Layer 1	20	0.87	0.94	1.01	0.04	20	0.78	0.84	0.93	0.03
Loc.4 of Ube Kosan Quarry	49	0.81	0.95	1.03	0.05	52	0.78	0.85	0.93	0.04
Ikumo Quarry	1	–	0.91	–	–	1	–	0.82	–	–

"*A. sylvaticus*" from Yunshui Cave has the same size as the present fossils in accordance with the description by HUANG and HOU (1984).

Comparisons with the European fossil species——

The present fossils are much smaller than *A. jeanteti* from the Early Pleistocene to Pliocene of Europe. According to MICHAUX (1967), the posterior cingulums of M^1 and M^2 of this species are rather similar to those of the "developed" variant of *A. speciosus*, but not so developed as in the present fossils. Moreover the lack of the medial anteroconid in M_1 of *A. jeanteti* is also a differential character. *A. dominans* is decidedly smaller than *A. jeanteti*, but generally larger than the present fossils. M^1 and M^2 of this species are three-rooted in contrast to the four-rooted condition in the same molars of the present fossils.

Concluding remarks on the comparisons——

The osteological and dental characters of the present fossils as already described are well coincident with those of the living *A. argenteus*, even if the morphological variation of the molars is taken into consideration. The above comparisons with several living and fossil species indicate that there are no species whose characters are better agreed with those of the present fossils than *A. argenteus*. Therefore the identification of the present fossils as *A. argenteus* is firmly ascertained.

Discussion

In contrast to *A. speciosus*, the taxonomic position of this species is rather stable in the opinions of mammalogists, because this species is rather distinctive in its external, osteological and dental characters as well as its smaller size. It is generally accepted that this species is endemic to the present Japan, and distributed in Hokkaido, Honshu, Shikoku, Kyushu and their adjacent small islands. The fossils of this species are also known exclusively from Japan.

The genus *Apodemus* is subdivided into three subgenera such as *Apodemus, Sylvaemus* and *Alsomys* by the presence or absence of the supraorbital ridges, number of mammae, numbers of roots of M^1 and M^2 and degree of the development of the labial anterocone in M^2 (ZIMMERMANN, 1962). *A. argenteus* is included in *Alsomys* as well as the East Asiatic species such as *A. speciosus, A. peninsulae, A. latronum, A. semotus* and *A. draco*, and the Himalayan species, *A. gurkha* THOMAS. However *A. argenteus* seems to have a peculiar position in this subgenus, because the diagnostic characters of the subgenus are partly lacking in this species (namely in *A. argenteus*, the supraorbital ridge is absent, and M^1 and M^2 are four-rooted). This species is rather similar to *A. microps* of the subgenus *Sylvaemus* in skull characters and size, as well as in numbers of roots of M^1 and M^2. However the patterns of the upper molars of *A. microps* are different from those of *A. argenteus*, as already mentioned.

As concerns the dental morphology of the genus *Apodemus*, the following characters are interpreted as primitive, when palaeontological evidences are taken into consideration:

(1) The posterostyle is absent or strongly reduced in M^1 and M^2.
(2) M^1 and M^2 are three-rooted instead of four.
(3) The posterior cingulum is well developed in M^1 and M^2.
(4) The labial anterocone is well developed in M^2.
(5) The posterior spurs of the anterostyle and labial anterocone are developed in M^1.

The character (1) is diagnostic to the genus *Parapodemus*, but not observed in the species of the genus *Apodemus*. The character (2) is found in the species of *Alsomys* except *A. argenteus*. In contrast to the other species of *Alsomys*, however, *A. argenteus* possesses the characters (3), (4) and (5) altogether. This fact suggests that this species is relatively primitive in dental morphology and possibly near to ancestral forms of the genus *Apodemus*. If the species of *Alsomys* were derived from a common ancestor, the lineage which leads to the living *A. argenteus* may be independent from the others. In this lineage, the evolutionary changes have possibly been slight, but the roots of M^1 and M^2 have increased from three to four. On the other hand, the three-rooted condition has been preserved in the other lineages of *Alsomys*.

The present study indicates that *A. argenteus* has flourished in Japan since the Middle Pleistocene as *A. speciosus*, while any allied form to *A. argenteus* is not found in the Late and Middle Pleistocene fossils of China. Because even the Middle Pleistocene fossils of *A. argenteus* are hardly different from the living animals, this species possibly arose from its ancestor in the periods earlier than the Middle Pleistocene.

The living *A. argenteus* exclusively inhabits in forests. Therefore the occurrence of this species in a fossil population is indicative of sylvan environments. Because almost all micro-mammalian fossil localities in Japan abundantly yield this species, it is inferred that such environments have been continuously existent since the Middle Pleistocene. This estimation is consistent with the vegetational conditions deduced from palaeobotanical evidences.

Genus ***Tokudaia*** KURODA, 1943

Remarks

This monospecific genus is represented by *T. osimensis* (ABE), which was first described by ABE (1933) as a new subspecies of *Rattus jerdoni* (BLYTH). Because *osimensis* bears several peculiar characters, TOKUDA (1941b) considered it as an independent species belonging to a new genus named *Acanthomys*, instead of *Rattus*. But TOKUDA's name was soon replaced by *Tokudaia* of KURODA in 1943, because the former name had been preoccupied by *Acanthomys* LESSON, 1842. In 1946, JOHNSON proposed *Tokudamys* on the spiny rat found in Okinawa Island. However it is synonymized with *Tokudaia*.

The present distribution of this genus is restricted to the only two islands of the Ryukyu Islands such as Amami-oshima Island and Okinawa Island*. It is interesting from biogeographical viewpoints, because the allied forms are not found in the adjacent areas such as the mainland of Japan, Korea, China and Taiwan. The Late Pleistocene and Holocene fossils of *Tokudaia* are known from Okinawa Island and Ie Island of the same islands (Table 108).

Tokudaia osimensis (ABE, 1933)

(Figs. 185–189)

Rattus jerdoni osimensis, ABE 1933, *Botany and Zoology*, **1**, 940–942.

Synonym (*living forms*) ——

Rattus jerdoni osimensis; ABE 1934, *Jour. Sci. Hiroshima Univ.*, Div. 1, **3**, 107–114.
Rattus jerdoni osimensis ABE; KURODA 1940, *Monogr. Japanese Mamm.*, 137–138.
Acanthomys osimensis (ABE); TOKUDA 1941, *Trans. Biogeogr. Soc. Japan*, **4**, 95.
Tokudaia osimensis (ABE); KURODA 1943, *Bull. Biogeogr. Soc. Japan*, **13**, 59–64.
Tokudamys osimensis muenninki; JOHNSON 1946, *Proc. Biol. Soc. Washington*, **59**, 169–172.
Tokudaia osimensis ABE; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian Mammals*,

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* Recently, HONDA *et al.* (1977) stated that *T. osimensis* from Amami-oshima was unlikely to be conspecific to that from Okinawa Island from the results of karyotype analysis, although they did not give a difinite taxonomic conclusion.

Table 108. Fossil localities of *Tokudaia osimensis*. Gohezu Cave (1) is situated in Ie Island, while the other five localities are in Okinawa Island.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
1. Gohezu Cave	*Tokudaia* aff. *osimensis*	Hasegawa *et al.* (1978)	Late Pleistocene or Holocene (uncertain).
2. Hinigushiku Shell-mound	*Tokudaia osimensis*	Kowalski & Hasegawa (1976)	Holocene.
3. Iso	*Tokudaia osimensis*	This paper	Late Pleistocene.
4. Gajanbira	*Tokudaia osimensis*	This paper	Ditto.
5. Kuteken	*Tokudaia osimensis*	This paper	Ditto.
6. Minatogawa Site	*Tokudaia osimensis*	Takai & Hasegawa (1971); Kowalski & Hasegawa (1976); Hasegawa (1980a); this paper	Late Pleistocene to Holocene.

558.
Tokudaia osimensis Abe; Imaizumi 1960, *Coloured Illustr. Mamm. Japan*, 152.

Synonym (*fossil forms*) ——

Tokudaia osimensis (Abe); Kowalski and Hasegawa 1976, *Bull. Nat. Sci. Mus.*, Ser. C, **2**, 37–38; from Minatogawa and Hinigushiku Shell Mound.

Tokudaia aff. *osimensis* (Abe); Hasegawa *et al.* 1978, *Research of Gohezu Cave in Ie Island, Okinawa Pref.*, 12–13; from Gohezu Cave.

Materials ——

Minatogawa

Excavated materials: 3 maxillae with M^1, M^2 and M^3 (KUJC100553, 100557, 100558); 3 maxillae with M^1 and M^2 (KUJC100579, 100612, 100613); 1 maxilla with M^1 (KUJC100598); 1 premaxilla with I (KUJC100554); 3 maxillae without teeth (KUJC100559, 100580, 100597); 31 isolated upper incisors (KUJC100623–100653); 6 isolated M^1 (KUJC100560, 100581–100583, 100599, 100600); 3 isolated M^2 (KUJC100561, 100584, 100615); 1 isolated M^3 (KUJC100601); 2 mandibles with I, M_1, M_2 and M_3 (KUJC100585, 100620); 2 mandibles with M_1, M_2 and M_3 (KUJC100569, 100621); 4 mandibles with I, M_1 and M_2 (KUJC100555, 100562, 100616, 100622); 3 mandibles with M_1 and M_2 (KUJC100563, 100595, 100602); 1 mandible with I and M_1 (KUJC100564); 5 mandibles with M_1 (KUJC100565, 100570, 100571, 100586, 100617); 3 mandibles with I (KUJC100566, 100567, 100603); 6 mandibles without teeth (KUJC100568, 100572, 100576, 100596, 100604, 100605); 34 isolated lower I (KUJC100654–100687), 10 isolated M_1 (KUJC100573, 100574, 100587, 100588, 100606–100608, 100614, 100618, 100619); 4 isolated M_2 (KUJC100575, 100609–100611); 2 isolated M_3 (KUJC100556, 100589).

Materials by surface collection: 3 isolated upper I (KUJC100688–100690); 1 mandible with I, M_1, M_2 and M_3 (KUJC100577); 1 mandible with I and M_2 (KUJC100578); 3 isolated lower I (KUJC100691–100693).

Kuteken

2 isolated upper I (KUJC100694, 100695).

Iso

2 isolated upper I (KUJC100696, 100697); 1 mandible with I, M_1 and M_2 (KUJC100590); 1 mandible with M_1 and M_2 (KUJC100592); 1 mandible with I and M_1 (KUJC100591); 6 isolated

lower I (KUJC100698–100703).

Gajanbira

1 mandible with I, M_1 and M_2 (KUJC100593); 1 mandible with M_1 and M_2 (KUJC100594); 1 isolated lower I (KUJC100704).

Diagnosis

Symphyseal eminence present on the lower border of mandible below mental foramen. Molars hypsodont; their general patterns resembling those of *Apodemus*. M^1 usually four-rooted; its labial anterocone, posterostyle and posterior cingulum well developed. M^2 also with four roots; its posterostyle and posterior cingulum well developed, but labial anterocone always lacking. M^3 three-rooted; its anterior lamina arranged obliquely to the transverse axis of crown; anterostyle easily connecting with this lamina in early stages of wear. Lower molars with two roots each; M_1 with a broad occlusal outline; its medial anteroconid well developed, so that its anterior chevron exhibits a "triforium" shape; middle chevron of M_1 generally showing an obtuse angle; in slightly worn teeth, posterior chevron of M_1 divided into hypoconid and entoconid by a median longitudinal groove; buccal accessory cusps of M_1 and M_2 poorly developed, which correspond to C1 and C3 in M_1, and to C2 only in M_2; entoconid of M_3 remarkably large, and with a semi-circular occlusal surface.

Description

Maxilla (Fig. 185) ——

The surface of the masseteric plate is flattened, and the small tubercle on its antero-inferior part seen in *Mus* and *Micromys* is lacking or inconspicuous as in *Apodemus* and *Rattus*. The alveolar part of the maxilla is concave, when the molars are removed. Corresponding to the number of roots of each molar, the alveolar pits of M^1 are generally four in number, and those of M^2 and M^3 are four and three respectively.

Mandible (Figs. 185, 186) ——

The mandible is morphologically similar to that of *Apodemus*. But in comparison with the Japanese species of *Apodemus*, it is larger and more heavily built. The mental foramen opens on the buccal face of the mandible somewhat anterior to M_1. The symphyseal eminence is clearly observed on the lower border of the mandible below the mental foramen. The upper masseteric crest is absent, but the lower masseteric crest is well developed. The alveolar part is remarkably concave, when the specimens without molars are observed. The protuberant area on the buccal face of the ascending ramus formed by the posterior end of the incisor is lower than the occlusal level of the lower molars. The mandibular foramen opens at the position slightly lower than this level. The lingual face of the ascending ramus is broadly concave below the central oblique ridge.

Incisor (Fig. 187) ——

The upper and lower incisors are normal. They have no longitudinal grooves on their enamel-covered surfaces. The orange colouration is sometimes preserved on

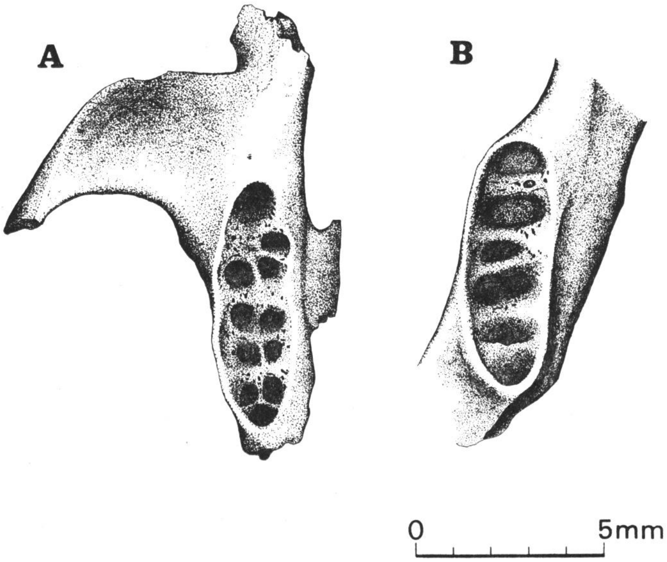

Fig. 185. *Tokudaia osimensis* from Minatogawa. Alveolar patterns on maxilla (A) and mandible (B). A, right maxilla (KUJC100559); B, left mandible (KUJC100566).

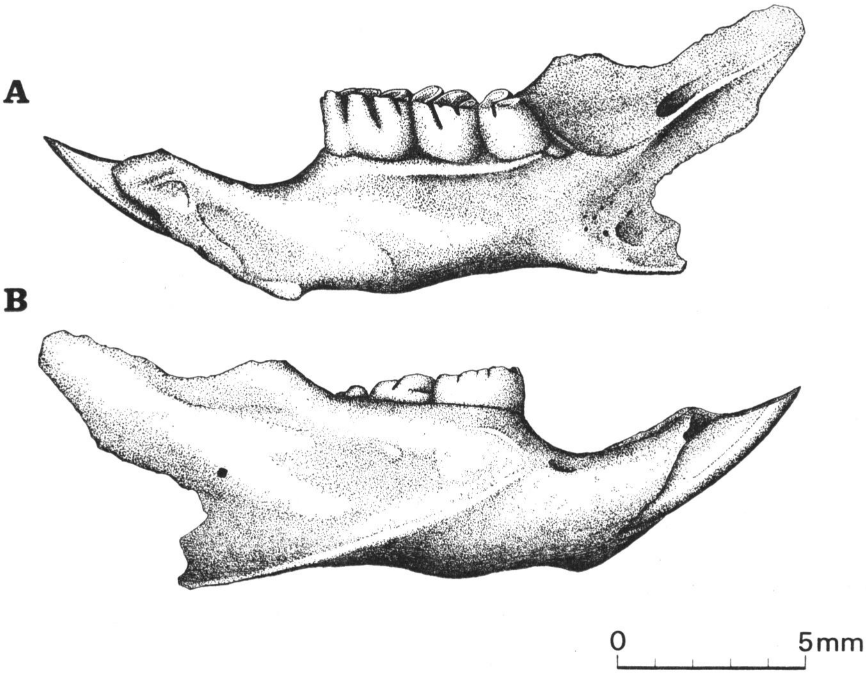

Fig. 186. *Tokudaia osimensis*. Right mandible with I, M_1, M_2 and M_3 from Minatogawa (KUJC100620). A, lingual view; B, buccal view.

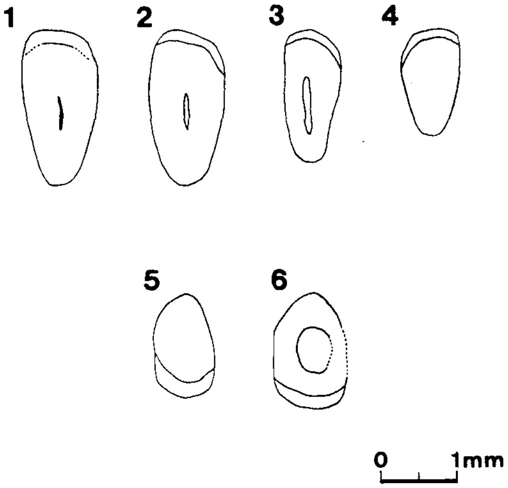

Fig. 187. Cross section of the incisors of *Tokudaia osimensis* from Minatogawa (1, 3–6) and Iso (2). 1–3, right upper incisors (KUJC100649, 100697 and 100641 respectively); 4, left upper incisor (KUJC100644); 5, 6, left lower incisors (KUJC100677 and 100665 respectively).

the surfaces. The cross section of the upper incisor shows an oval shape elongated dorso-ventrally, which is similar to those of the Japanese *Apodemus* and *Rattus*. The cross section of the lower incisor is also oval-shaped but proportionately broader, which resembles that of *Rattus* rather than that of *Apodemus*.

General characters of the molars ——

The molars are characteristically hypsodont. Their hypsodonty is more advanced than that of *Apodemus, Micromys, Mus* and *Rattus* (Fig. 188), but as advanced as that of *Rhagamys* illustrated by SCHAUB (1938, Fig. 17). The general patterns of the molars are similar to those of *Apodemus* and *Micromys* rather than *Mus* and *Rattus* in having well-developed posterostyle in M^1 and well-defined medial anteroconid in M_1. Excepting the change by wear, the variation in the molar patterns is generally slight.

M^1 ——

The prestyle and precingulum are always absent. The lingual anterocone is set near to the labial anterocone rather than to the anterostyle, so that the connection of the occlusal surfaces between the lingual anterocone and labial anterocone is completed earlier than that between the former and anterostyle. The anterostyle is situated somewhat posterior to the labial anterocone. A weak spur is usually present on the posterior face of the anterostyle, but any spur is not found on the same face of the labial anterocone. On the anterior face of the middle chevron, the groove between the protocone and enterostyle is more distinct than that between the protocone and paracone. The occlusal surfaces of the paracone and metacone are confluent earlier

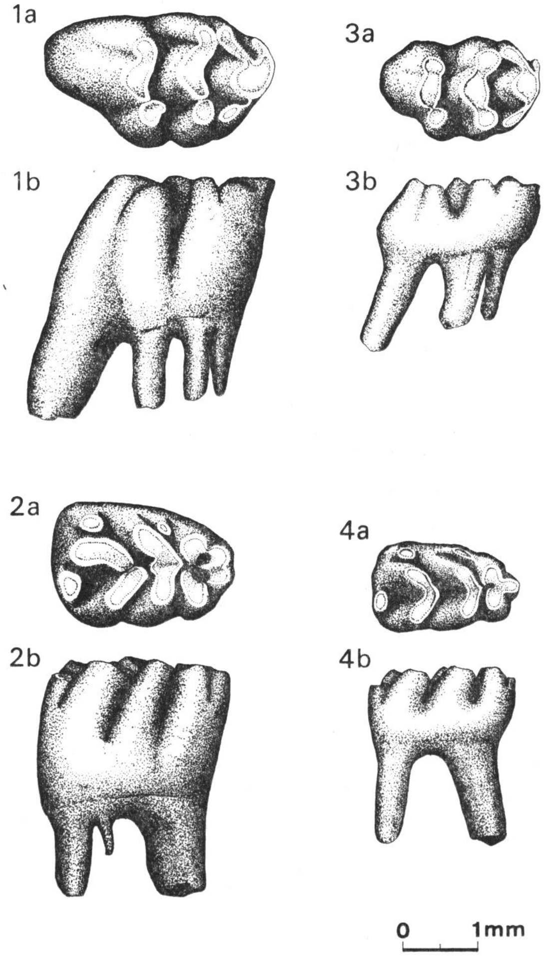

Fig. 188. Left M^1 and M_1 of *Tokudaia osimensis* (1 and 2) and *Apodemus speciosus* (3 and 4), showing the differences in hypsodonty and pattern between these two species (1a, 2a, 3a, 4a, occlusal view; 1b, 2b, 3b, 4b, lingual view). 1, M^1 from Minatogawa (KUJC100560; the postero-buccal root is somewhat damaged); 2, M_1 from the same locality as 1 (KUJC100587); 3, M^1 from Layer 1 of Locality 3 of Ube Kosan Quarry (KUJC97202); 4, M_1 from the same layer and locality as 3 (KUJC97638).

than those of the enterostyle and posterostyle. The posterior cingulum is well developed and attached on the postero-buccal face of the hypocone. The valley between the posterior cingulum and the ridge connecting the hypocone with the metacone is narrow but deep. It becomes an isolated pit in later stages of wear.

M^1 is usually four-rooted (in seven specimens out of nine). The anterior root is the largest, and has an oval cross section elongated antero-posteriorly. The other three roots are much smaller, and have round cross sections. Of these, the postero-buccal

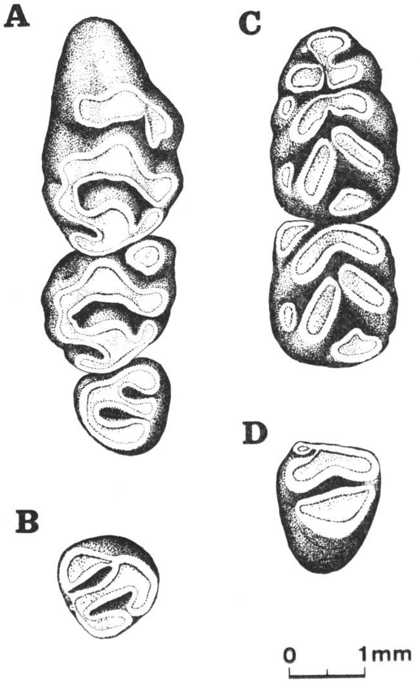

Fig. 189. *Tokudaia osimensis* from Minatogawa. A, right M^1, M^2 and M^3 (KUJC100558); B, left M^3 (KUJC100601); C, left M_1 and M_2 (KUJC100563); D, left M_3 (KUJC100621).

root approximates to the antero-lingual one in size, whereas the postero-lingual root is somewhat smaller. In one specimen (KUJC100582), the antero-lingual and postero-lingual roots are fused into one stout root which is elongated antero-posteriorly. Consequently, the total number of roots decreases to be three. In this specimen, the postero-buccal root becomes thicker than that of other specimens. In another specimen (KUJC100583), the antero-lingual root seems to be divided into two roots, although all the roots of this specimen are badly damaged. Therefore, in this case, the total number of roots seems to be five.

M^2——

The labial anterocone is lacking. The morphology of the anterior and posterior chevrons is identical with that of the corresponding chevrons of M^1. The posterior cingulum is well developed as in M^1. Four roots with round cross sections are always present. The postero-lingual root is the smallest of the four, but the other three are approximately equal in size.

M^3——

The occlusal outline of the crown is round rather than triangular. The general pattern of the crown is similar to the "*speciosus* type" or "*giliacus* type" proposed by the present author in the section of *Apodemus* of this paper (Fig. 160), although the anterostyle is more isolated in the former type, and the outline is more triangular in the latter type.

Table 109. Ratio of crown width against crown length (W/L) in M_1 of the fossil *Tokudaia osimensis* from Minatogawa, Gajanbira and Iso. For comparison, the data on the living specimens of *Apodemus* collected from Gifu and Aichi Prefectures are also given (*A. speciosus* from Gujohachiman, Ikeda, Myogata and Mikawa Heights; *A. argenteus* from the same localities except Ikeda). Abbreviations as in Table 38.

		WIDTH / LENGTH			
	N	min	m	max	SD
Tokudaia osimensis (fossil)	32	0.602	0.661	0.721	0.030
Apodemus speciosus (living)	65	0.555	0.610	0.655	0.022
Apodemus argenteus (living)	68	0.546	0.608	0.697	0.029

The occlusal surface of the anterostyle easily connects with that of the protocone in early stages of wear. The anterior lamina formed by the protocone and enterostyle is arranged obliquely to the transverse axis of the crown. The axis of the valley between the anterior and posterior laminas is also obliquely arranged. This valley opens postero-lingually or postero-buccally. The former and latter types correspond to the "normal type" and "abnormal type I" of *Apodemus speciosus* by the present author (Table 88). As the crown is worn, this valley becomes a closed pit. The same change is observed in the valley between the anterostyle and anterior lamina.

M^3 is three-rooted. These roots are nearly equal in size.

M_1——

The occlusal outline is somewhat broader than that of the Japanese *Apodemus*. The ratio of crown width against crown length (W/L) is usually more than 0.63 (Table 109). The medial anteroconid is well developed as in *Apodemus*. In slightly worn teeth, it is sometimes divided into two cusps with nearly the same size, or sometimes has a small accessory cusp on its buccal face. As the wear of the crown is advanced, the occlusal surface of the medial anteroconid connects with those of the lingual and labial anteroconids to form the "triforium-shaped" anterior chevron. One or two weak spurs are rarely observed on the posterior face of this chevron. The protoconid and metaconid are well confluent to form the middle chevron even in slightly worn teeth. In worn specimens, the anterior and middle chevrons are connected with each other at their medial parts. The angle of the middle chevron is usually obtuser than that of the posterior chevron. In extreme cases, it approaches to 180°, but in other cases, it comes near to the angle of the posterior chevron. A posterior spur is sometimes observed at the medial part of the posterior face of the middle chevron.

In slightly worn teeth, the entoconid is barely separated from the hypoconid by a narrow median groove. Such a separation of these cusps is characteristic to the slightly worn teeth of the present fossils, but it is not observed in any specimen of *Apodemus* examined in this paper. The anterior tip of the entoconid is somewhat anterior to that of the hypoconid. As the wear is advanced, the groove soon disappears, and these two cusps are jointed anteriorly to form the posterior chevron. The posterior cingulum is oval or triangular in occlusal view.

The buccal accessory cusps are poorly developed, and their variation is limited. C1 and C3 are always present, but others never appear. In almost all the specimens (23 out of 24), C3 is smaller than or as large as C1, and situated at the buccal entrance of the valley between the anterior and middle chevrons. Owing to its columnar shape, its occlusal surface is round or oval, but is never elongated antero-posteriorly. These specimens obviously belong to the morphotype A of *Apodemus* proposed by the present author (Fig. 178). Only in one specimen (KUJC100586), C3 is elongated antero-posteriorly. Therefore this specimen belongs to the morphotype C of *Apodemus*. The predominancy of the morphotype A is a discriminative character of M_1 of the present fossils from that of the Japanese *Apodemus* where this morphotype is generally rare.

M_1 usually has two roots. The anterior root has an oval cross section whose long axis is somewhat oblique to the longitudinal axis of the crown. On the other hand, the posterior root is elongated transversely, and rectangular in cross section. In two specimens (KUJC100574 and 100587) out of nine, a small additional root is observed immediately anterior to the posterior root (Fig. 188).

M_2——

The anterior and posterior chevrons are morphologically identical with the corresponding chevrons of M_1. A weak spur is rarely observed on the anterior face of the posterior cingulum. In 12 specimens out of 13, the buccal accessory cusp is represented by C2 only which is situated at the buccal entrance of the valley between the anterior and posterior chevrons. Consequently, these specimens are assignable to the morphotype D of *Apodemus* by the present author (Fig. 179). But another specimen (KUJC100610) belongs to the morphotype A, because it lacks any buccal accessory cusps.

Two roots are always present, namely anterior and posterior roots. The former is smaller than the latter. They have rectangular cross sections elongated transversely.

M_3——

The crown comprises two basic parts such as the anterior chevron and well-developed entoconid. In slightly worn teeth, a longitudinal groove is observable in the medial part of the anterior chevron. It separates the protoconid from the metaconid. This groove soon disappears by the wear of the crown. The small labial anteroconid is always attached on the anterior face of the protoconid. The entoconid is remarkably large, and has nearly the same width as the anterior chevron. Its occlusal surface is semi-circular. The transverse valley between the anterior chevron and entoconid tapers at both lateral ends to form isthmuses. The lingual isthumus is narrower and shallower than the buccal one. Consequently, the occlusal surface of the anterior chevron is united with that of the entoconid at the lingual side earlier than at the buccal side.

M_3 is two-rooted. The anterior root is smaller than the posterior one. The former has an elliptical cross section elongated transversely. The latter extends postero-ventrally and has a round cross section.

Measurements

The measurements of the mandibles and molars are shown in Tables 110 and 111 respectively. In comparison with the Japanese fossil and living murids, their sizes are much larger than those of *Apodemus, Micromys* and *Mus,* but rival those of *Rattus.* On the other hand, the sizes are considerably smaller than those of *Diplothrix.*

Comparisons

The present fossil materials are well coincident with the living *Tokudaia osimensis* in dental and osteological characters. Moreover there are no significant differences between these materials and the fossils of *T. osimensis* described by KOWALSKI and HASEGAWA (1976) and HASEGAWA *et al.* (1978). Therefore these materials are referable to *T. osimensis.* This conclusion is firmly supported by the following comparisons with numerous living and fossil murids known from the Palaearctic and Oriental Regions.

Comparisons with the living Palaearctic genera ——

Four genera such as *Rattus* (*sensu stricto*), *Mus*, *Apodemus* and *Micromys* are representative murids in the present Palaearctic Region. The fossil materials described here are different from *Rattus* and *Mus* in having hypsodont molars, well-developed posterostyle and posterior cingulum in M^1 and M^2, and also well-developed medial anteroconid in M_1. Except the hypsodonty, these characters are also found in *Micromys.* However this genus is distinct from the present fossils in having smaller size, less swollen cusps, less developed posterior cingulums in M^1 and M^2, well-developed labial anterocone in M^2, and slenderer outline and "X-pattern" of M_1. On the other hand, the molar patterns of *Apodemus* are generally similar to those of the present fossils in the arrangement and degree of the development of each cusp. However the crowns of the molars of *Apodemus* are remarkably lower than those of the present fossils.

Comparisons with the living Oriental genera ——

Numerous living murid genera are known from the Oriental Region. Because their classification was recently revised by several works, the new classification compiled by HONACKI *et al.* (1982) is adopted here. Moreover, more recent data provided by MUSSER (1982a, b, c) and MUSSER and NEWCOMB (1983) are added. The following comparisons are based mainly on the descriptions of THOMAS (1898), TATE (1936), AOKI and TANAKA (1941), MISONNE (1969), MUSSER (1972, 1973, 1981a, b; 1982a, b, c), MUSSER and GORDON (1981), MUSSER *et al.* (1981), and MUSSER and

Table 110. Measurements of the mandibles of *Tokudaia osimensis* in mm. The numbers on the left side correspond to those in Fig. 72.

	Minatogawa (excavated specimens)									
	KUJC 100555	KUJC 100562	KUJC 100563	KUJC 100564	KUJC 100565	KUJC 100566	KUJC 100567	KUJC 100568	KUJC 100569	KUJC 100570
4. Length of the horizontal ramus	–	–	–	11.51±	–	11.04	11.61	10.40	–	–
5. Length of the diastema	–	–	–	5.88±	–	–	5.48	5.13	5.47	–
12. Height of the horizontal ramus at M_1	3.79	–	3.61	3.72	3.08	3.58±	2.85±	–	–	–
13. Ditto at M_3	3.31	–	2.92	3.57	–	3.30	2.88	–	–	3.18
14. Maximum thickness of the horizontal ramus	2.92	–	2.55	2.80	2.66	2.75	2.57	2.45	–	–
15. Length of the molar row (M_1 to M_3) at the crowns	–	–	–	–	–	–	–	–	6.01	–
16. Ditto at the alveoli	6.15	–	6.01	5.99	–	–	6.42	6.15	–	6.32
17. Length of the molar row (M_1 to M_2) at the crowns	4.49	4.42	4.46	–	–	–	–	–	4.41	–
18. Ditto at the alveoli	4.20	–	4.28	4.18	4.35	–	4.31	4.33	4.35	4.48

	Minatogawa (excavated specimens)									Minatogawa (surface coll.)		Gajanbira		Iso		
	KUJC 100572	KUJC 100585	KUJC 100586	KUJC 100595	KUJC 100602	KUJC 100616	KUJC 100620	KUJC 100621	KUJC 100622	KUJC 100577	KUJC 100578	KUJC 100593	KUJC 100594	KUJC 100590	KUJC 100591	KUJC 100592
4.	–	–	–	–	–	–	–	–	11.54	–	–	–	–	–	–	–
5.	–	–	–	–	–	–	5.69±	–	5.28	–	–	–	–	–	5.32	–
12.	–	4.23	–	3.78	–	–	3.46	–	–	–	3.84	–	–	–	3.56	–
13.	–	–	–	3.84	–	–	3.15	–	3.12	3.15	3.25	3.19	–	–	–	–
14.	–	2.89	–	3.01	–	–	3.09	–	2.63	–	–	–	–	2.82±	2.83	–
15.	–	5.73	–	–	–	–	6.07	6.06	–	6.17	–	–	–	–	–	–
16.	–	5.61	6.46	6.09±	–	–	–	–	6.48	–	5.79±	6.79	–	–	–	–
17.	–	4.01	–	4.19	4.37±	4.72	4.33	4.35	4.78	4.31	–	4.68±	4.91	4.33	–	4.36±
18.	4.68	3.87±	4.67	4.06±	–	4.53	4.25±	–	4.55	–	3.92±	–	4.71	–	–	4.37±

Table 111. Measurements of the molars of *Tokudaia osimensis* in mm. es, excavated specimens; sc, surface collection.

SPECIMEN NUMBER	LENGTH	WIDTH
M^1		
Minatogawa (es)		
KUJC100553	3.26	1.97
KUJC100557	3.08	1.88
KUJC100558	3.04	1.86
KUJC100560	3.03	1.82
KUJC100579	3.17	1.93
KUJC100581	3.19	1.90
KUJC100582	3.09	1.86
KUJC100583	3.28	1.91
KUJC100598	3.06	1.85
KUJC100599	3.13	1.83
KUJC100600	3.20	1.84
KUJC100612	–	1.81
KUJC100613	3.03	1.83
M^2		
Minatogawa (es)		
KUJC100553	2.05	1.86
KUJC100557	1.85	1.78
KUJC100558	1.76	1.77
KUJC100561	1.99	1.80
KUJC100579	1.91	1.78
KUJC100584	2.07	1.82
KUJC100613	1.79	1.74
KUJC100615	1.91	1.75
M^3		
Minatogawa (es)		
KUJC100553	1.35	1.38
KUJC100557	1.41	1.23
KUJC100558	1.22	1.36
KUJC100601	1.30	1.33
M_1		
Minatogawa (es)		
KUJC100555	2.57	1.76
KUJC100562	2.58	1.78
KUJC100563	2.58	1.72
KUJC100564	2.43	1.57
KUJC100565	2.53	1.67
KUJC100569	2.59	1.77
KUJC100570	2.59	1.64
KUJC100571	2.56	1.72
KUJC100573	2.76	1.73
KUJC100574	2.50	1.62
KUJC100585	2.30	1.66
KUJC100586	2.64	1.71
KUJC100587	2.58	1.64
KUJC100588	2.59	1.76
KUJC100595	2.39	1.66
KUJC100602	2.54	1.67
KUJC100606	2.60	1.64
KUJC100607	2.43	1.57
KUJC100614	2.39	1.68
KUJC100616	2.64	1.90
M_1 (continued)		
Minatogawa (es)		
KUJC100617	2.54	1.53
KUJC100618	2.62	1.64
KUJC100619	2.61	1.61
KUJC100620	2.47	1.74
KUJC100621	2.48	1.56
KUJC100622	2.68	1.78
Minatogawa (sc)		
KUJC100577	2.53	1.67
Gajanbira		
KUJC100593	2.68	1.86
KUJC100594	2.78	1.78
Iso		
KUJC100590	2.55	1.75
KUJC100591	2.56	1.63
KUJC100592	2.50	1.68
M_2		
Minatogawa (es)		
KUJC100555	1.92	1.77
KUJC100562	1.88	1.82
KUJC100563	1.97	1.72
KUJC100569	1.82	1.81
KUJC100575	1.96	1.69
KUJC100585	1.84	1.76
KUJC100609	1.86	1.75
KUJC100610	2.11	1.76
KUJC100611	2.07	1.77
KUJC100616	2.02	1.89
KUJC100620	1.89	1.77
KUJC100621	1.91	1.68
KUJC100622	2.09	1.97
Minatogawa (sc)		
KUJC100577	2.02	1.72
Gajanbira		
KUJC100593	2.15	1.86
KUJC100594	2.14	1.90
Iso		
KUJC100592	1.85	1.71
M_3		
Minatogawa (es)		
KUJC100556	1.91	1.33
KUJC100585	1.84	1.35
KUJC100589	1.95	1.33
KUJC100620	1.85	1.40
KUJC100621	1.78	1.36
Minatogawa (sc)		
KUJC100577	1.98	1.38

NEWCOMB (1983).

Among the Oriental murids, four genera such as *Celaenomys, Chrotomys, Crunomys* and *Rhynchomys* have very peculiar molar patterns which were called "basin-shaped molars" by MISONNE (1969). *Apomys* also has unique molars which are characterized by slenderer M^1 and M^2 with simple structures, and by simple M_1 with only two transverse laminas and a posterior cingulum. Moreover *Crateromys* and *Pithecheir* are unique in the absence or strong reduction of the metacone in M^1 and M^2 as well as in having well-developed posterostyle in the same molars. In the molars of *Bandicota, Nesokia* and *Phloeomys*, cusps are completely fused into straight transverse ridges. Consequently these genera are easily discriminated from the present fossils by the above-mentioned characters.

The absence of the posterostyle in M^1 and M^2, and that of the medial anteroconid in M_1 is characteristic to the following genera: *Abditomys, Anonymomys, Archboldomys, Berylmys, Bullimus, Chiromyscus, Cremnomys, Dacnomys, Diomys, Hadromys, Kadarsanomys, Leopoldamys, Maxomys, Millardia, Niviventer, Sundamys* and *Tryphomys*. On the other hand, *Golunda, Haeromys, Limnomys* and *Palawanomys* have M^1 without the posterostyle, but M_1 with small medial anteroconid. In *Batomys* and *Srilankamys*, at least, there are no posterostyle in M^1 and M^2. Therefore these genera are easily distinguishable from the present fossils even by these characters only, because the present fossils are characterized by M^1 with well-developed posterostyle and by M_1 with also well-developed medial anteroconid. These characters of the present fossils are shared by the following genera: *Carpomys, Chiropodomys, Hapalomys, Lenothrix, Vandeleuria* and *Vernaya*. However their molars are obviously different from those of the present fossils. The differential characters are described as follows:

In *Carpomys*, the chevrons of each molar are straighter and lamina-shaped. The lingual cusps of M^1 are relatively smaller than the other cusps, and are well separated from the central cusps. The posterior cingulums of M^1 and M^2 are better developed and connect to the lingual part of the hypocone to form the additional fourth lamina. The middle and posterior laminas of M^1 are distinctly separated from each other. Moreover, the anterior lamina of M^1 has a more complicate structure.

Chiropodomys is much smaller than the present fossils. It has more elongate posterostyle in M^1 and M^2, well-developed anterostyle in M^2, more complicate pattern of M^3, and better developed buccal accessory cusps or cingulums in M_1 and M_2.

The molars of *Hapalomys* have very peculiar patterns which are characterized by well-separated cusps. These cusps never form chevron-shaped ridges by their coalescence. M^1 and M^2 of this genus have more squarish outlines. Additionally, M_1 and M_2 have well-developed buccal accessory cusps which usually rival the main cusps in size.

Lenothrix is somewhat similar to the present fossils in molar patterns. In its M^1 and M^2, however, the posterior spur of the paracone is well developed and sometimes becomes an independent cusp. Moreover its M^3 is decidedly different. Namely this tooth is so elongated that its occlusal outline exhibits a rectangular shape. Its pattern is more complicate, which comprises the anterostyle, two well-separated laminas and a distinct posterior cingulum.

Vandeleuria is much smaller than the present fossils. Its M^1 and M^2 have poorly developed metacone, and its M^3 exhibits a more cuspidate pattern. Furthermore its M_1 and M_2 have slenderer outlines. The anterior and middle chevrons of its M_1 are easily coalescent at their medial parts to form the "X-pattern" which is typically seen in *Mus* and *Micromys*.

Vernaya is also smaller than the present fossils. In its M^2, the labial anterocone is well developed. The pattern of its M^3 is simpler, which is composed of two transverse laminas only. The medial anteroconid of its M_1 is smaller and well separated from the lingual and labial anteroconids. The "X-pattern" in its M_1 is easily formed as in *Vandeleuria*.

Summarizing up these comparisons, it can be said that the molar patterns of the above-mentioned genera are not coincident with those of the present fossils.

Comparisons with the living murids of Sulawesi ——

In his taxonomic and biogeographic works, TOKUDA (1941a, b) pointed out the close relationship between some murids of the Ryukyu Islands and those of Sulawesi (Celebes). For instance, he stressed the affinity of *Tokudaia osimensis* of the former with "*Rattus beccarii*" of the latter. Therefore it is necessary to compare the present fossils with "*R. beccarii*" and other murids of Sulawesi.

As for "*R. beccarii*," MUSSER (1981a) allocated this species to his new genus *Margaretamys* in his revision of the Indo-Malayan murids. Moreover he added two new species to this genus, which were named *M. elegans* and *M. parvus*. Judging from his description and figure, the molar patterns of *M. beccarii* are dissimilar to those of the present fossils. The following characters of *M. beccarii* are never observed in the present fossils:

1. In M^1 and M^2, an additional cusp or a spur is present on the posterior face of the paracone. Moreover the protocone has a cusp-like spur on its lingual face. The enterostyle is separated from the protocone or weakly connects with it. The posterostyle is absent. The posterior cingulum is lamina-like and attached on the postero-lingual face of the hypocone.
2. In M^3, the posterior cingulum is present. It is small but conspicuous.
3. Each chevron of the lower molars is straighter.

These differential characters are also observed in *M. elegans* and *M. parvus*.

Excluding the genera already compared, eight genera can be chosen from MUSSER's list of the murids of Sulawesi (1981b, p. 137). They are *Bunomys, Echiothrix, Eropeplus, Lenomys, Melasmothrix, Paruromys, Taeromys* and *Tateomys*. The molar patterns of these genera are easily distinguishable from the present fossils by the following criteria: 1, hypsodonty of the molars; 2. presence or absence of the posterostyle in M^1 and M^2; 3. presence or absence of the posterior cingulum in M^1 and M^2; if present, degree of its development; 4. presence or absence of the posterior cingulum in M^3; 5. presence or absence of the medial anteroconid in M_1; if present, degree of its development; 6. degree of the development of the buccal accessory cusps or number of them in M_1 and M_2; 7. number of roots in each molar.

Consequently, it can be concluded that there are no genera among the murids of Sulawesi whose molars are similar to those of the present fossils.

Comparisons with the Chinese and Indian fossil murids ——

The subsequent comparisons are focused on the Chinese and Indian fossil genera, such as *Antemus, Chardinomys, Karnimata, Orientalomys, Parapelomys, Parapodemus* and *Progonomys*. These comparisons are based on the descriptions of SCHAUB (1938), TEILHARD (1940), BRUIJN and MEULEN (1975), JACOBS (1978) and JACOBS and LI (1982). Several extant genera such as *Apodemus, Bandicota, Golunda, Micromys, Mus, Rattus* and *Vernaya* are also known from these areas as the Neogene and Quaternary fossils. But in order to avoid duplication, they are omitted from the subsequent comparisons.

Of these genera, *Antemus, Karnimata, Parapelomys* and *Progonomys* have brachydont molars, and lack the posterostyle in M^1 and M^2. M^1 of *Chardinomys* is unique in the diagonal arrangement of the cusps. The posterostyle is also absent from its M^1 and M^2. M^1 and M^2 of *Orientalomys* exhibit remarkable stephanodonty and are also characterized by the absence of the posterostyle. *Parapodemus* has *Apodemus*-like molar patterns, but the posterostyles of its M^1 and M^2 are absent or inconspicuous. Consequently these fossil genera are easily discriminated from the present fossils even by these characters only, although several minor differential characters are also existent between them.

Comparisons with the European fossil murids ——

Numerous fossil genera have been described from the European Neogene and Quaternary sediments. They are represented by *Anthracomys, Castillomys, Occitanomys, Orientalomys, Paraethomys, Parapodemus, Progonomys, Rhagamys, Rhagapodemus, Stephanomys* and *Valerymys*. Of these, *Orientalomys, Parapodemus* and *Progonomys* are excluded from the subsequent comparisons, because they are compared in the preceding section.

M^1 and M^2 of *Anthracomys, Castillomys, Occitanomys, Paraethomys, Stephanomys* and *Valerymys* are characterized by the absence of the posterostyle, and by the absence or reduction of the posterior cingulum. In addition to these characters, stephanodonty is typically observed in the molars of *Castillomys* and *Stephanomys*. Therefore these genera are easily discriminated from the present fossils.

On the other hand, the molar patterns of *Rhagamys* and *Rhagapodemus* are rather similar to the present fossils, because their patterns are of basically the *Apodemus*-type. Moreover the molars of *Rhagamys* are as hypsodont as those of the present fossils as already described. However these two genera are distinguishable from the present fossils by the following dental characters:

Rhagamys differs from the present fossils in having poorly developed buccal cusps in M^1 and M^2, a remarkable posterior spur of the labial anterocone in M^1, the metacone which readily connects with the paracone instead of the hypocone in M^1, the different structure of M^3 where the central valley opens antero-lingually, and three buccal accessory cusps instead of two in M_1. *Rhagapodemus* also differs from the present fossils in having smaller size, less hypsodont molars, more posteriorly situated anterostyle in M^1, well-developed labial anterocone in M^2, and more numerous buccal accessory cusps in M_1 and M_2.

Concluding remarks on the comparisons——

In conclusion, there are no genera whose dental characters are better coincident with those of the present fossils than *Tokudaia* among the numerous living and fossil murid genera compared above. Among these genera, however, it is also suggested that the present fossils are rather similar to *Apodemus, Rhagapodemus* and *Rhagamys* in molar pattern.

Discussion

Tokudaia osimensis is an interesting animal which has peculiar dental, osteological and external characters in comparison with the living murids of the adjacent areas. As for its origin, two different opinions were previously presented. One is TOKUDA's (1941a), and another is MISONNE's (1969). TOKUDA considered that *T. osimensis* had been derived from the common ancestor to *Margaretamys beccarii* of Sulawesi. This opinion is, however, unprobable from the viewpoint of the present author, because the molar patterns of *Margaretamys* are considerably different from those of *Tokudaia* as already mentioned. In order to confirm these observations, the detailed comparisons on the cranial morphology will be requested between these two genera, as recent authors did on other murids (for example, MUSSER 1981a).

On the other hand, MISONNE insisted the oceanic drift of this animal from Luzon, the Philippines. But this opinion is also untenable, because there are no murids in the Philippines whose molar patterns are similar to *T. osimensis*, and because no positive data which are indicative of the oceanic drift of mammals have been obtained in the Ryukyu Islands.

In contrast to these opinions, the present author infers the affinity and origin of *T. osimensis* as follows: As already mentioned, the molar patterns of this species are similar to those of *Apodemus, Rhagapodemus* and *Rhagamys*. On the other hand, the hypsodonty of this species is so advanced as that of *Rhagamys*. *Apodemus, Rhagapodemus* and *Rhagamys* are considered to be closely related to each other, and can be allocated to

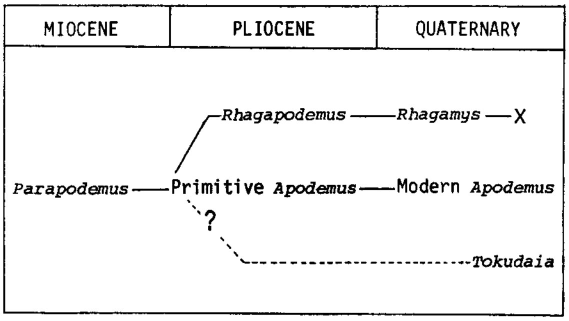

Fig. 190. Suggested phylogeny of *Tokudaia*. X, extinction.

a single group. From the above-mentioned similarities in dental morphology, it is probable that *T. osimensis* is also included in this group. According to CHALINE and MEIN (1979), *Rhagamys* was derived from *Rhagapodemus* in the Early Pleistocene, and the latter branched off from the *Parapodemus-Apodemus* lineage in the Late Miocene. The evolutionary trend from *Rhagapodemus* to *Rhagamys* is represented by the acquisition of hypsodonty and the modification of molar patterns. Because *Rhagamys* is an insular form of the Mediterranean, these changes seem to be related to the isolation of this animal into islands. It is interesting that *Tokudaia* is also an insular form of the Ryukyu Islands. The hypsodonty of *Tokudaia* may have been obtained by the same process.

Tokudaia possibly arose from the *Parapodemus-Apodemus* lineage, and evolved parallel to the *Rhagapodemus-Rhagamys* lineage (Fig. 190). The separation of the Ryukyu Islands from the continent is a main cause of such a evolutionary change. The direct ancestor which links *Tokudaia* to the primitive species of *Apodemus* has been hitherto unknown. However the present author believes that it will be found in the Miocene or Pliocene sediments of China.

Genus ***Diplothrix*** THOMAS, 1916

Remarks

This genus is represented by a single species, *legata*, whose present distribution is restricted to only three islands of the Ryukyu Islands such as Amami-oshima Island, Tokunoshima Island and the northern part of Okinawa Island. This large spinous rat was first described by THOMAS (1906a) as a new species of *Lenothrix*. In 1916, however, he transferred it to a new genus, *Diplothrix*, proposed by himself. Although ELLERMAN and MORRISON-SCOTT (1951) and IMAIZUMI (1960) regarded it as a subgenus of *Rattus*, several authors gave it a generic rank (KURODA, 1940; TOKUDA, 1941b; MISONNE, 1969; MUSSER and BOEADI, 1980; HONACKI *et al.*, 1982). It seems better to treat *Diplothrix* as a full genus, because several Southeast Asiatic murids which were formerly included in *Rattus* should be separated generically from *Rattus*.

Diplothrix legata (THOMAS, 1906)

(Fig. 191–193)

Lenothrix legata, THOMAS 1906, *Ann. Mag. Nat. Hist.*, Ser. 7, **17**, 88–89

Synonym (*living forms*) ——

Mus bowersii var. *okinavensis*; NAMIE 1909, *Zool. Mag.*, **21**, 455–457.
Lenothrix legata THOMAS; AOKI 1915, *Nipponsan Nezumika* (*Japanese Muridae*), 73–75.
Diplothrix legata; THOMAS 1916, *Jour. Bombay Nat. Hist. Soc.*, **24**, 404.
Lenothrix legata THOMAS; KISHIDA 1924, *Honyudobutsu Zukai* (*Monogr. Japanese Mamm.*), 138–139.
Diplothrix legata (THOMAS); KURODA 1940, *Monogr. Japanese Mamm.*, 161–162.
Diplothrix legata (THOMAS); TOKUDA 1941, *Trans. Biogeogr. Soc. Japan*, **4**, 116.
Rattus legatus THOMAS; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian Mammals*, 576.
Rattus legata THOMAS; IMAIZUMI 1960, *Coloured Illustr. Mamm. Japan*, 156–157.

Synonym (*fossil forms*) ——

Rattus cf. *legata* (THOMAS); HASEGAWA *et al.* 1973, *Mem. Nat. Sci. Mus.*, (6), 47; from Amagawa-do Cave and Tanabaru Cave.

Diplothrix legata (THOMAS); KOWALSKI and HASEGAWA 1976, *Bull. Nat. Sci. Mus.*, Ser. C, **2**, 44–45; from Minatogawa Site, Tanabaru Cave and Amagawa-do Cave.

Materials ——

Minatogawa (excavated material)

1 isolated upper I (KUJC100713).

Gajanbira

4 isolated upper I (KUJC100708, 100709, 100710 and one unnumbered specimen of the OSHIRO Collection); 1 isolated M^1 (KUJC100705); 2 mandibles with I, M_1, M_2 and M_3 (KUJC100706 and one unnumbered specimen of the OSHIRO Collection); 1 mandible with M_1, M_2 and M_3 (unnumbered specimen of the OSHIRO Collection); 1 mandible with I, M_1 and M_2 (unnumbered specimen of the OSHIRO Collection); 2 isolated lower I (KUJC100711, 100712), 1 isolated M_1 (KUJC100707).

Diagnosis

Size much larger than those of *Tokudaia osimensis* and *Rattus rattus*; but patterns and hypsodonty of molars similar to those of the latter species. M^1 with well-developed labial anterocone, but lacking posterostyle and posterior cingulum; mandible heavily built; medial anteroconid absent from M_1 which has one or two buccal accessory cusps; M_2 with only one buccal accessory cusp; labial anteroconid distinct in M_2 as well as in M_3; entoconid of M_3 remarkably large.

Description

Mandible (Fig. 191) ——

The mandible is stoutly built. In lateral view, the angle of diastema (a in Fig. 191) is about 90°. The mental foramen opens on the buccal face immediately anterior to M_1. The inner face of the horizontal ramus is rugose in the symphyseal part. The lower masseteric crest is distinct, but the upper masseteric crest is absent. The symphyseal eminence is present below the mental foramen, but it is inconspicuous.

Incisor (Fig. 192) ——

The upper and lower incisors are normal in shape. They always lack any grooves. The anterior part of the enamel-covered surface is pigmented in orange. The upper incisor has an elliptical cross section which elongates supra-inferiorly. The cross section of the lower incisor is similarly shaped, but its lower part somewhat broadens laterally.

M^1 ——

The occlusal outline is oval. Neither prestyle nor precingulum is present. The labial anterocone is well developed, and as large as the anterostyle. These cusps are arranged on the same transverse line which is slightly posterior to the lingual anterocone. A weak spur is observed on the posterior face of the labial anterocone. The transverse valley between the anterior and middle chevrons is deep and broad. Corresponding to the position of the cusps of the anterior chevron, the paracone and enterostyle are set on the same line which is somewhat posterior to the protocone.

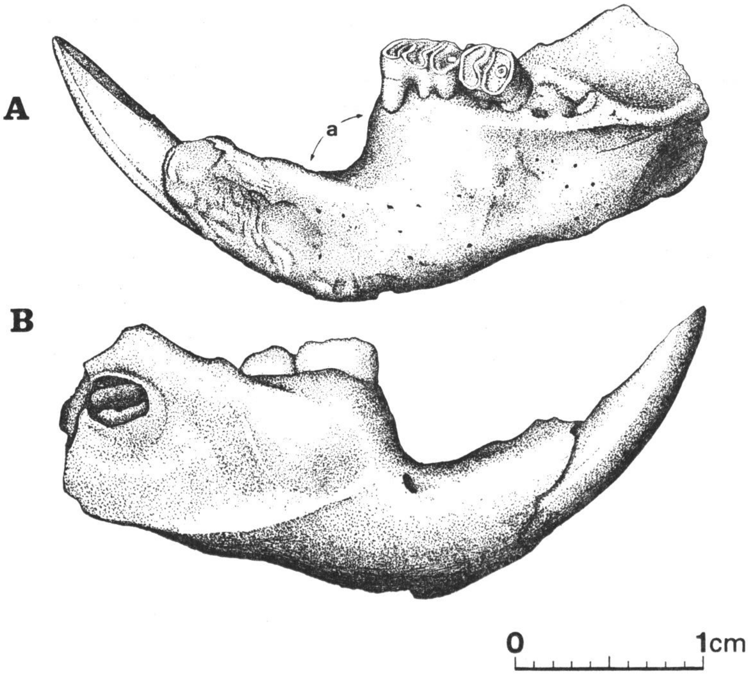

Fig. 191. *Diplothrix legata* from Gajanbira. Right mandible with I, M_1 and M_2 (OSHIRO Collection). A, lingual view; B, buccal view; a, angle of diastema. M_2 of this specimen is secondarily tilted lingually.

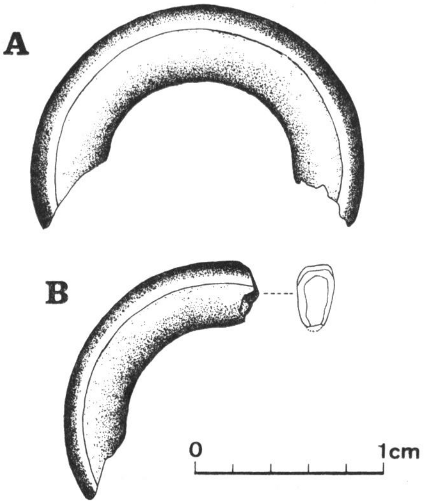

Fig. 192. Upper incisors of *Diplothrix legata,* A, lateral view of the left upper incisor from Gajanbira (KUJC100708). B, lateral view of the left upper incisor from Minatogawa (KUJC100713; the cross section observed at the broken end is also shown).

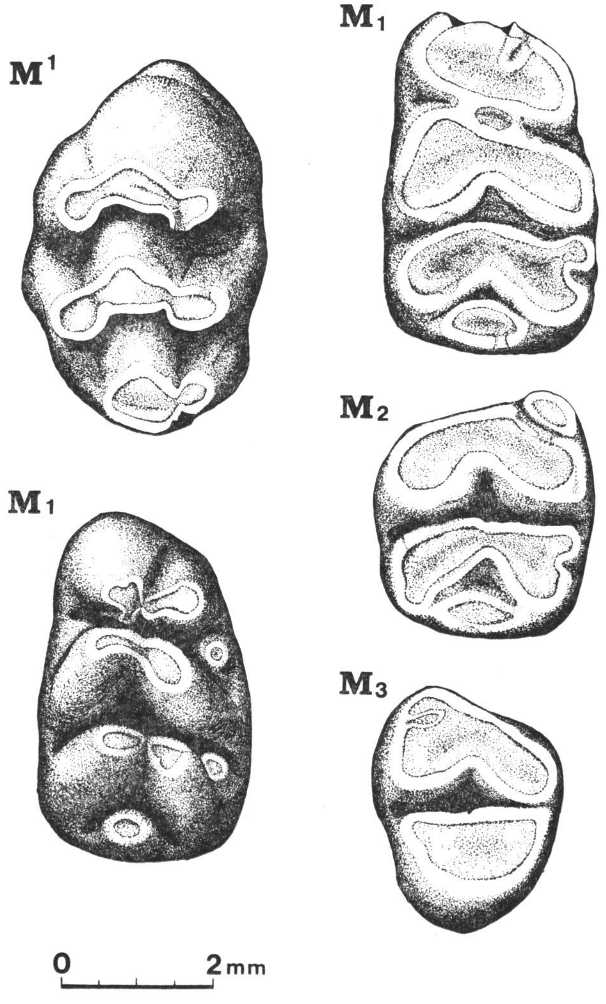

Fig. 193. Molars of *Diplothrix legata* from Gajanbira. M^1, left M^1 (KUJC100705); M_1 (left bottom), right M_1 (KUJC100707); M_1 (right top), right M_1 (Oshiro Collection); M_2, right M_2 (Oshiro Collection, the same individual as the preceding right M_1); M_3, left M_3 (Oshiro Collection).

The posterior chevron which comprises only two cusps such as large hypocone and well-defined metacone is well separated from the middle chevron by a deep transverse valley. Although this valley slightly shallows at the lingual and buccal parts, it is assumed that the occlusal surface of the middle chevron is hardly confluent with that of the posterior chevron at these parts even in severely worn teeth. The lingual and postero-buccal faces of the hypocone are slightly swollen to form weak ridges. They are considered to be traces of the posterostyle and posterior cingulum, or to show an incipient stage of the development of these cusps.

M_1 ——

The occlusal outline is rectangular but rather broad. Observed in the slightly worn tooth (KUJC100707), the lingual main cusps (lingual anteroconid, metaconid and entoconid) are remarkably higher than the buccal main cusps (labial anteroconid, protoconid and hypoconid).

The medial anteroconid is completely absent. Therefore the anterior chevron is composed of only two cusps such as the lingual anteroconid and labial anteroconid which connect posteriorly. Each of these cusps has a weak posterior spur. The central valley between these cusps is narrow but distinct. It extends somewhat obliquely to the long axis of the crown, and opens anteriorly.

The middle and posterior chevrons are normal in shape, and have neither anterior mure nor medial mure. The transverse valley between the anterior and middle chevrons is deep and somewhat broadens laterally. Because it deepens medially, the occlusal surfaces of these chevrons are never confluent medially to form the "X pattern." The other transverse valley between the middle and posterior chevrons is also deep, and remarkably broadens and deepens medially. The posterior cingulum is oval in occlusal view, and well separated from the posterior chevron. One or two accessory cusps are observed on the buccal side of the crown. They are round or oval in occlusal view, but never elongate antero-posteriorly.

M_1 seems to have more than two roots.

M_2 ——

The occlusal outline is squarish. The labial anteroconid is relatively small, but distinct. The anterior chevron, posterior chevron and posterior cingulum are morphologically equivalent to the corresponding parts of M_1. Only one accessory cusp is present at the buccal entrance of the transverse valley between the anterior and posterior chevrons.

M_3 ——

The occlusal outline is rather longer than broad. The length of the crown rivals that of M_2. The anterior margin of the crown is straight, and considerably oblique to the transverse axis of the crown. The labial anteroconid is distinct and oval in occlusal view. The transverse valley between the anterior chevron and entoconid deepens medially. The entoconid is very large, and has a semicircular occlusal surface. Accessory cusps are not observed in any part of the crown.

Measurements

The measurements of the mandibles and molars are given in Table 112. The sizes of these materials are the largest among the Japanese murids. They are near to those of the living *Diplothrix legata*, although they are slightly larger than the latter.

Comparisons

Comparisons with the living murids ——

Table 112. Measurements of the mandibles and molars of *Diplothrix legata* from Gajanbira in mm. The numbers on the left side correspond to those in Fig. 72. UNS, unnumbered specimens of the OSHIRO Collection.

		SPECIMEN NUMBER					
		KUJC 100705	KUJC 100706	KUJC 100707	UNS	UNS	UNS
MANDIBLE							
4. Length of the horizontal ramus		–	–	–	–	–	23.04
5. Length of the diastema		–	–	–	–	–	11.69
12. Height of the horizontal ramus at M_1		–	–	–	8.64±	–	10.32±
13. Ditto at M_3		–	6.63	–	–	6.48±	6.63±
14. Maximum thickness of the horizontal ramus		–	–	–	5.35	–	5.35
15. Length of the molar row (M_1 to M_3) at the crowns		–	–	–	10.86	10.55±	–
16. Ditto at the alveoli		–	11.15±	–	10.96	11.14±	11.92
17. Length of the molar row (M_1 to M_2) at the crowns		–	–	–	7.52±	7.51±	7.79±
18. Ditto at the alveoli		–	8.17±	–	7.70±	8.15±	8.11
MOLAR							
M^1	Length	4.87	–	–	–	–	–
	Width	3.21	–	–	–	–	–
M_1	Length	–	–	4.59	4.42±	4.46±	4.52
	Width	–	–	2.83	2.88	–	2.90
M_2	Length	–	3.16	–	3.21	3.15	3.32
	Width	–	2.94	–	2.89	2.92	2.89
M_3	Length	–	3.14	–	3.48	3.27	–
	Width	–	2.60	–	–	2.57	–

The present fossil materials are first compared with the numerous living genera known from the Palaearctic and Oriental Regions. They are *Abditomys, Anonymomys, Apodemus, Apomys, Archboldomys, Bandicota, Batomys, Berylmys, Bullimus, Carpomys, Celaenomys, Chiromyscus, Chrotomys, Crateromys, Cremnomys, Crunomys, Dacnomys, Diomys, Diplothrix, Golunda, Hadromys, Haeromys, Hapalomys, Kadarsanomys, Lenothrix, Leopoldamys, Limnomys, Maxomys, Micromys, Millardia, Mus, Nesokia, Niviventer, Palawanomys, Phloeomys, Pithecheir, Rattus, Rhynchomys, Srilankamys, Sundamys, Tokudaia, Tryphomys, Vandeleuria* and *Vernaya.* The following dental characters observed in the present fossils are important for the comparisons with these genera:

1. The transverse cusp rows in each molar form chevron-shaped crests.
2. In M^1, the posterostyle and posterior cingulum are lacking. The middle chevron of the same tooth is distinctly separated from the posterior chevron by the deep transverse valley, so that these chevrons seem not to connect with each other at both lateral parts even in worn stages.
3. The medial anteroconid is absent from M_1. One or two buccal accessory cusps are present in M_1. The anterior and middle chevrons of this tooth do not form the "X-pattern" even in worn stages.

4. The labial anteroconid is present in M_2 and M_3.

Among the above-listed genera, only four genera such as *Bullimus, Diplothrix, Rattus* and *Tryphomys* share all of these characters with the present fossils. Therefore, the detailed comparisons with these four genera are requested.

In the molars of *Bullimus,* the chevrons are straighter than those of the present fossils. The labial anterocone of M^1 is inconspicuous, and broadly merged with the lingual anterocone (the former cusp is well-defined, and relatively discrete from the latter cusp in the present fossils). The posterior cingulum of M^1 is sometimes present (it is absent in the present fossils).

The molar patterns of *Rattus* are similar to those of the present fossils, as far as the available M^1, M_1, M_2 and M_3 are concerned. However *Rattus* is distinguishable from the present fossils in having smaller size, shorter M_3 relative to M_2 and a wider angle of diastema in mandibles.

Tryphomys is also distinguished from the present fossils in the following characters : 1. The size is smaller. 2. The chevrons of each molar are straighter. 3. In M_1, the lingual anteroconid is much larger than the labial anteroconid (such a size difference is not so conspicuous in the present fossils). 4. In M_1 and M_2, the posterior cingulum is smaller.

In contrast with these three genera, the dental and osteological characters of *Diplothrix* show strong resemblance to those of the present fossils. The sizes of both forms are also similar.

Outside the Palaearctic and Oriental Regions, the comparisons with murids of Sulawesi are important, when TOKUDA's theory (1941 a, b) is taken into consideration, as already mentioned in the section of *Tokudaia osimensis.* The following nine genera native to Sulawesi are compared with the present fossils : *Bunomys, Echiothrix, Eropeplus, Lenomys, Margaretamys, Melasmothrix, Paruromys, Taeromys* and *Tateomys.* Among these, the above-mentioned four dental characters of the present fossils are observable in the molars of *Bunomys, Paruromys* and *Taeromys.* However they are distinguished from the present fossils by the following characters.

In regard to *Bunomys,* the size is smaller, and the chevrons of each molar are slightly straighter. The labial anterocone and metacone are broadly confluent with the lingual anterocone and hypocone respectively in M^1 (the connections of these cusps are not so strong in the present fossils). The relative length of M_3 is shorter. In M^1 of *Paruromys,* an additional cusp is characteristically observed behind the enterostyle, and a remarkable spur is present behind the paracone. Moreover the labial anterocone of this tooth is broadly merged with the lingual anterocone, and its posterior cingulum is present in many cases. However these characters are never found in M^1 of the present fossils. The molars of *Taeromys* have straighter chevrons than those of the present fossils. In M^1 of this genus, the labial anterocone is inconspicuous or absent, but it is relatively large and independent from the lingual anterocone in the present fossils. In M_2 of this genus, the labial anteroconid is smaller than that in the present fossils.

Table 113. Fossil localities of *Diplothrix legata*. The first four localities (1–4) are situated in Okinawa Island, whereas the remaining ones are in Miyako Island.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
1. Hamabaru Shellmound	*Diplothrix legata*	Tokijin Hamabaru Shellmound Research Group (1977)	Holocene.
2. Sakihigawa Shellmound	*Diplothrix legata*	Naora (1944)	Holocene; no descriptions are given.
3. Gajanbira	*Diplothrix legata*	This paper	Late Pleistocene.
4. Minatogawa Site	*Diplothrix legata*	Takai & Hasegawa (1971); Kowalski & Hasegawa (1976); Hasegawa (1980a); this paper	Late Pleistocene to Holocene.
5. Tanabaru Cave	*Diplothrix legata*	Hasegawa *et al.*(1973); Kowalski & Hasegawa (1976)	Geological age is uncertain; Pleistocene?
6. Amagawa-do Cave	*Diplothrix legata*	Hasegawa *et al.* (1973); Kowalski & Hasegawa (1976)	Ditto.
7. Pinza-Abu Cave	*Diplothrix legata*	Hasegawa (1985)	Late Pleistocene.

Comparisons with the fossil murids ——

Among the numerous fossil genera known from China, India and Europe, the following representative genera are compared with the present fossils: *Antemus*, *Anthracomys*, *Castillomys*, *Chardinomys*, *Karnimata*, *Occitanomys*, *Orientalomys*, *Paraethomys*, *Parapelomys*, *Parapodemus*, *Progonomys*, *Rhagamys*, *Rhagapodemus*, *Stephanomys* and *Valerymys*. The comparisons with these genera reveal that none of them are coincident with the present fossils in dental morphology.

Concluding remarks on the comparisons ——

The present fossils are characterized by the large size and *Rattus*-like molar patterns. The above-mentioned comparisons with numerous genera indicate that the osteological and dental characters of *Diplothrix* as well as its size are most similar to those of the present fossils. Therefore they are assignable to *Diplothrix*. Because this genus is represented by only one species, *legata*, as already mentioned, their identification as *D. legata* is most reliable.

Discussion

In Okinawa Island, the recent distribution of *Diplothrix legata* is extremely confined to the small areas of its northern part. They are the southern limit of its distribution. However the fossils of this species are known from six localities which are entirely beyond this limit (Table 113). Especially the occurrences from Tanabaru Cave, Amagawa-do Cave and Pinza-Abu Cave in Miyako Island are noticeable, because this island is about 250 km southwest of Okinawa Island. This fact indicates that the former distribution of this species is much wider than the present condition.

In agreement with the original allocation by THOMAS (1906a), TOKUDA (1941a, b) stated that *Diplothrix* was related to *Lenothrix* of Sumatra or *Lenomys* of Sulawesi, and added that its affinity to the latter was stronger. But as already compared, both genera are quite different from *Diplothrix* in dental characters. The main differences are listed below.

1. The molar patterns are generally more complicate in *Lenothrix* and *Lenomys*.
2. The posterostyle and posterior cingulum are present in M^1 of *Lenothrix* and *Lenomys*. The posterior spurs of the enterostyle and paracone are also present in the same tooth of these genera (these spurs are sometimes represented by small cusps).
3. The medial anteroconid is present in M_1 of *Lenothrix* and *Lenomys*.

Because these differences are considerably great as murid molars, the close alliance of *Diplothrix* to *Lenothrix* and *Lenomys* is unprobable.

On the other hand, ELLERMAN and MORRISON-SCOTT's treatment (1951) of *Diplothrix* as a subgenus of *Rattus* is indicative of its affinity to the latter genus. As a matter of fact, the molar patterns of M^1, M_1, M_2 and M_3 of *Diplothrix* resemble those of *Rattus* (the present fossil materials are represented by these molar kinds). But the other molars such as M^2 and M^3 of *Diplothrix* have more complicate patterns than those of *Rattus*, so that the former is dissimilar to the latter (these molars are observable in the living *Diplothrix*). Therefore the above-mentioned subgeneric treatment of *Diplothrix* is problematic.

Diplothrix possibly belongs to an independent lineage which branched off from a primitive murid in earlier geological ages. In contrast to TOKUDA's opinion, the lineage of *Diplothrix* seems to be near to that of *Rattus*, but far from those of *Lenothrix* and *Lenomys*. The phylogeny of this unique genus will be sufficiently understood, when the fossil murids from China, India and Southeast Asia will be investigated in detail.

Genus ***Rattus*** FISCHER, 1803

Remarks

The definition of this extensive genus is still unstable. The recent treatments are inclined to exclude many species which were formerly included in this genus. The present author mainly employs the classification provided by HONACKI *et al.* (1982). He also accepts the more recent opinions by MUSSER (1982a) and MUSSER and NEWCOMB (1983), where several species included in *Rattus* by HONACKI *et al.* are transferred to newly established genera, *Abditomys* and *Sundamys*.

The fossil records of "*Rattus*" are rather numerous in the Quaternary sediments of East Asia (Figs. 194–197; Tables 114–117). The fossils with smaller size obtained from northern China have been mostly identified as "*R. rattus*," whereas those with larger size from southern China have been usually assigned to "*R. edwardsi*." These identifications are, however, oversimplified and far from sufficient. MISONNE (1969) already stated "the Chinese forms described by PEI (1936) and TEILHARD (1938) from

Fig. 194. Early Pleistocene fossil localities of "*Rattus*" in East Asia. 1, Locality 12 of Choukoutien; 2, Chiachiashan; 3, Weinan. For detailed explanation see Table 114.

Table 114. Early Pleistocene fossil localities of "*Rattus*" in East Asia. The numbers on the left side correspond to those in Fig. 194.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
CHINA			
1. Locality 12 of Choukoutien	*Rattus rattus*	Teilhard (1938)	Originally described as "*Epimys rattus*." Misonne (1969) considered that this identification was doubtful.
2. Chiachiashan	*Rattus* cf. *rattus*	Pei (1930)	Originally described as "*Mus* cf. *rattus*."
3. Weinan	cf. *Rattus* sp.	Xue (1981), Jacobs & Li (1982)	

the Pleistocene of Choukoutien as *Epimys rattus** do not belong at all to that species." He pointed out that these fossils were close to *Maxomys niviventer* (=*Niviventer niviventer* in the present treatment). Moreover he stated that the occurrence of *Rattus edwardsi*

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* *Epimys* Trouessart, 1881 is preoccupied by *Rattus* Fischer, 1803.

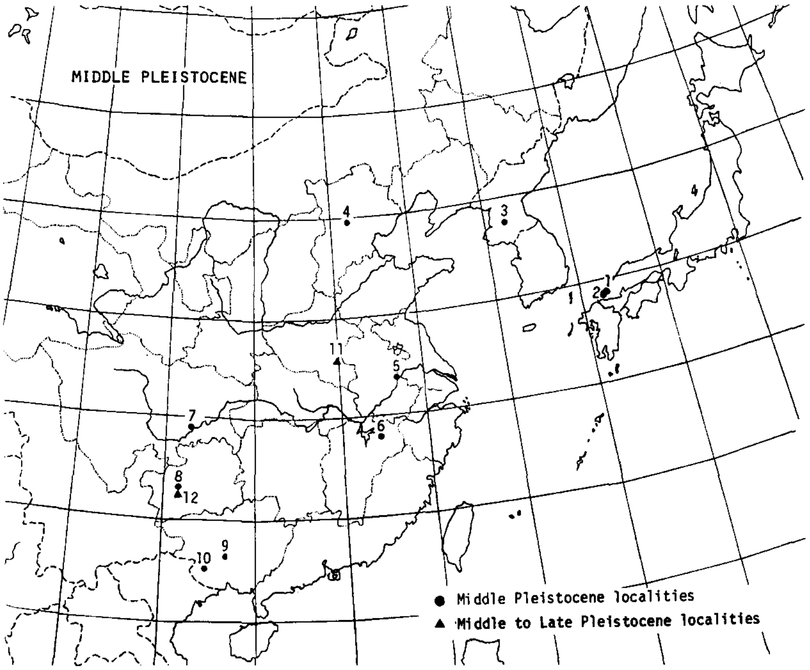

Fig. 195. Middle Pleistocene fossil localities of "*Rattus*" in East Asia (including two Middle to Late Pleistocene localities). 1, Ikumo Quarry; 2, Locality 4 of Ube Kosan Quarry; 3, Sangwon Komunmoru Cave; 4, Choukoutien (Localities 1, 3, 9 and 21); 5, Hexian; 6, Yungshan Cave at Loping; 7, Koloshan; 8, Chihchin; 9, Wuming; 10, Tahsin; 11, Hsintsai; 12, Baiyanjiao Cave. For detailed explanation see Table 115.

(=*Leopoldamys edwardsi* in the present treatment) was also found in the descriptions of "*Epimys rattus*" from Choukoutien by YOUNG (1934) and TEILHARD (1938). He concluded that *Rattus rattus* had not been present before historical times outside Malaya-Java. Although the present author does not always agree with MISONNE's opinion, the fossil forms formerly assigned to *Rattus* should be revised from the recent knowledge.

The fossil materials described here are referable to *Rattus* of the present treatment by the following dental characters as well as the size, proportion of each molar and occlusal outlines of the molars.

1. The hypsodonty is moderate.
2. Each molar has chevron-shaped laminas which are well separated from each other.
3. Neither posterostyle nor posterior cingulum is present in M^1 and M^2. The posterior spurs are also absent from the paracone and enterostyle in the same teeth, so that the middle and posterior laminas of M^1 and the corresponding parts of M^2 are not confluent even in worn stages.

Table 115. Middle Pleistocene, and Middle to Late Pleistocene fossil localities of "*Rattus*" in East Asia. The numbers on the left side correspond to those in Fig. 195.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
MIDDLE PLEISTOCENE			
JAPAN			
1. Ikumo Quarry	*Rattus* sp.	Hasegawa (1963, 1966); Kowalski & Hasegawa (1976)	
2. Locality 4 of Ube Kosan Quarry	*Rattus* aff. *norvegicus*	This paper	
KOREA			
3. Sangwon Komunmoru Cave	*Rattus rattus*	Kim & Kim (1974)	
CHINA			
4. Locality 1 of Choukoutien	*Rattus rattus*	Young (1934); Kahlke & Chow (1961)	Young described it as "*Epimys rattus*." Misonne (1969) considered that this identification was doubtful.
4. Locality 3 of Choukoutien	*Rattus rattus*	Pei (1936)	Pei described it as "*Epimys rattus*." Misonne (1969) considered this identification was also doubtful.
4. Locality 9 of Choukoutien	*Rattus rattus*	Teilhard (1936)	Originally assigned to "*Epimys rattus*." No descriptions are given.
4. Locality 21 of Choukoutien	*Rattus rattus*	Chia *et al.* (1959)	Ditto.
5. Hexian	*Rattus rattus* *Rattus norvegicus* *Rattus edwardsi*	Huang *et al.* (1982); Zheng (1983)	No descriptions are given.
6. Yungshan Cave at Loping	*Rattus rattus*	Huang & Ji (1963)	Young (1947) described the same species from a cave of "Loping."
7. Koloshan	*Rattus rattus* *Rattus* cf. *edwardsi*	Young & Liu (1950)	Originally described as "*Epimys rattus* and *Epimys* cf. *edwardsi*."
8. Chihchin	*Rattus rattus*	Hsu *et al.* (1957)	
9. Wuming	*Rattus* cf. *edwardsi*	Ji (1977)	No descriptions are given.
10. Tahsin	*Rattus rattus*	Han (1982)	Ditto.
MIDDLE TO LATE PLEISTOCENE			
CHINA			
11. Hsintsai	*Rattus rattus*	Pei (1956)	Originally described as "*Epimys rattus*."
12. Baiyanjiao Cave	*Rattus rattus*	Li & Cai (1986)	No descriptions are given.

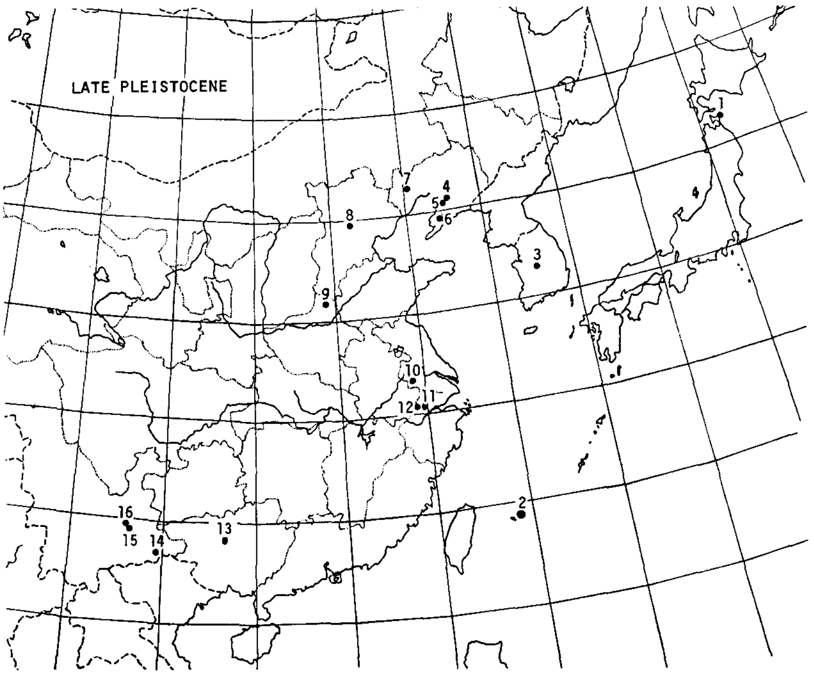

Fig. 196. Late Pleistocene fossil localities of "*Rattus*" in East Asia. 1, Shiriya Quarry; 2, Ishisukuyama; 3, Turubong Cave; 4, Xiaogushan; 5, Jinniushan; 6, Gulongshan; 7, Gezidong; 8, Upper Cave of Choukoutien; 9, Hsiaonanhai; 10, Shenxiandong Cave at Lishui; 11, Fenghuangshan; 12, Huayan Cave at Xitianmu; 13, Xiandong Cave at Duan; 14, Xianrendong Cave at Xizhou; 15, Longtanshan First Cave at Kunmin; 16, Sanjiacun. For datailed explanation see Table 116.

4. In M^2, the labial anterocone is usually absent, or if present, it is strongly reduced.
5. M^3 and M_3 are relatively large.
6. The medial anteroconid is absent from M_1, where the "X-pattern" is hardly formed. The anterior lamina has nearly the same width as the middle lamina, and the lingual anteroconid is larger than the labial anteroconid in the same tooth.
7. One or two buccal accessory cusps are present in M_1, while one buccal accessory cusp is present in M_2.
8. In M_1 and M_2, the posterior cingulum is normal in shape and not reduced in size. The labial anteroconid is present in M_2 and M_3.

The geological ages of the present materials are considered to be the Middle Pleistocene and Holocene*. Although all of the Middle Pleistocene materials are isolated teeth, they can be treated as a single species from their occurrence (obtained from a single horizon of a single locality), size, proportion of each tooth and other

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* A fossil femur which is referable to *Rattus* is newly found from the Late Pleistocene horizon (Horizon N) of Kannondo Cave Site. *It is not listed in* KAWAMURA*'s preliminary reports (1979a, 1980 etc.).*

Table 116. Late Pleistocene fossil localities of "*Rattus*" in East Asia. The numbers on the left side correspond to those in Fig. 196.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
JAPAN			
1. Shiriya Quarry	*Rattus norvegicus*	Nakajima (1958); Hasegawa (1966, 1972); Naora (1972); Kowalski & Hasegawa (1976)	
2. Ishisukuyama	*Rattus rattus*	Hasegawa & Nohara (1978)	No descriptions are given.
KOREA			
3. Turubong Cave	*Rattus norvegicus* *Rattus rattus*	Lee (1983); Sohn (1984)	No descriptions are given.
CHINA			
4. Xiaogushan	*Rattus rattus*	Zhang *et al.* (1985)	No descriptions are given.
5. Jinniushan	*Rattus* sp.	Archaeological United Team (1976); Zhang (1981)	Ditto.
6. Gulongshan	*Rattus rattus*	Zhow *et al.* (1984)	Ditto.
7. Gezidong	*Rattus rattus*	Archaological Team of Provincial Museum of Liaoning and IVPP (1975); Zhang (1981)	Ditto.
8. Upper Cave of Choukoutien	*Rattus rattus*	Pei (1940)	Originally described as "*Epimys rattus*."
9. Hsiaonanhai	*Rattus* sp.	Chou (1965)	
10. Shenxiandong Cave at Lishui	*Rattus rattus*	Li & Lei (1980)	
11. Fenghuangshan	*Rattus rattus*	Han & Zhang (1978)	No descriptions are given.
12. Huayan Cave at Xitianmu Mountain	*Rattus rattus*	Zhang (1984)	
13. Xiandong Cave at Duan	*Rattus* cf. *subcristata*	Wu *et al.* (1976)	No descriptions are given.
14. Xianrendong Cave at Xizhou	*Rattus*	Chen & Qi (1978)	Ditto.
15. Longtanshan First Cave at Kunmin	*Rattus* sp.	Zhang *et al.* (1978)	Ditto.
16. Sanjiacun	*Rattus* cf. *edwardsi* *Rattus* cf. *niviventer*	Qiu *et al.* (1984)	

dental characters. They are assigned to *Rattus* aff. *norvegicus* by the similarity to *R. norvegicus*. But some differences from that species are also observable, which suggest the possibility of the subspecific or even specific distinction from the recent *R. norvegicus*. On the other hand, the Holocene materials are collected from different horizons of two fossil localities. They are divided into two groups here, and are described separately. One is represented by two maxillae with molars including M^1 which are

Fig. 197. Holocene fossil localities of "*Rattus*" in East Asia. 1, Kitoragawa Site; 2, Kannondo Cave Site; 3, Makurazino-ana Cave and Koziki-ana Cave; 4, Shimohieda Site; 5, Nodae-do; 6, Nongpo-ri; 7, Anyang; 8, Yuyao; 9, Zhenpiyan; 10, Gazo. For detailed explanation see Table 117.

diagnostic for the specific determination. Another is also represented by the materials without diagnostic parts. The former and latter are assigned to *R. norvegicus* and *R.* sp. respectively.

Rattus norvegicus (BERKENHOUT, 1769)

(Fig. 198)

Mus norvegicus, BERKENHOUT 1769, *Outlines Nat. Hist. Great Britain and Ireland,* **1,** 5.

Synonym (*living forms*; *restricted to the references treating the Japanese materials*)

Epimys norvegicus (ERXLEBEN); AOKI 1915, *Nipponsan Nezumika* (*Japanese Muridae*), 60–65.

Rattus norvegicus (ERXLEBEN); KISHIDA 1924, *Honyudobutsu Zukai* (*Monogr. Japanese Mamm.*), 132–136.

Rattus norvegicus (ERXLEBEN); WATANABE 1937, *Occ. Pap. Ibaraki Agr. St.,* (2), 45–49.

Rattus norvegicus norvegicus (ERXLEBEN), *R. n.* var. *hibernicus* (THOMPSON), *R. n.* var. *otomoi* YAMADA, *R. n.* var. *albinus* (HATAI), *R. n. longicaudus* MORI and *R. n. caraco* (PALLAS); KURODA 1940, *Monogr. Japanese Mamm.,* 143–147.

Rattus norvegicus norvegicus (BERKENHOUT); TOKUDA 1941, *Trans. Biogeogr. Soc. Japan,* **4,** 106–110.

Rattus norvegicus ERXLEBEN; IMAIZUMI 1949, *Nat. Hist. Japanese Mamm.,* 273–274.

Rattus norvegicus BERKENHOUT; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian*

Table 117. Holocene fossil localities of "*Rattus*" in East Asia. The numbers on the left side correspond to those in Fig. 197.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
JAPAN			
1. Kitoragawa Site	*Rattus* sp.	This paper	
2. Kannondo Cave Site	*Rattus norvegicus* *Rattus* sp.	Kawamura (1978, 1979a); this paper	
3. Makurazino-ana Cave	*Rattus norvegicus* or *Rattus rattus*	Shikama & Okafuji (1958); Kowalski & Hasegawa (1976)	
3. Koziki-ana Cave	*Rattus* sp.	Shikama & Okafuji (1958)	No descriptions are given.
4. Shimohieda Site	*Rattus norvegicus*	Hanamura (1985)	
KOREA			
5. Nodae-do	*Rattus norvegicus*	Sohn (1984)	No descriptions are given.
6. Nongpo-ri	*Rattus norvegicus*	Sohn (1984)	Ditto.
CHINA			
7. Anyang	*Rattus rattus*	Teilhard & Young (1936)	Originally assigned to "*Epimys rattus*."
8. Yuyao	? *Rattus*	Huang & Cao (1978)	No descriptions are given.
9. Zhenpiyan	*Rattus norvegicus*	Li & Han (1978)	
10. Gazo	*Rattus* sp.	Huang (1980)	No descriptions are given.

Mammals, 588–590.
Rattus norvegicus (BERKENHOUT); KURODA 1953, *Nippon Jurui Zusetsu* (*Monogr. Japanese Mamm.*), 89.
Rattus norvegicus BERKENHOUT; IMAIZUMI 1960, *Coloured Illustr. Mamm. Japan*, 155-156.
Rattus norvegicus; CORBET 1978, *The Mammals of the Palaearctic Region*, 140.

Synonym (*fossil forms*; *restricted to the fossils found in Japan*) ——
Rattus norvegicus (BERKENHOUT); KOWALSKI and HASEGAWA 1976. *Bull. Nat. Sci. Mus.*, Ser. C, **2**, 43–44; from Shiriya Quarry.

Materials ——
One left maxilla with M^1, M^2 and M^3, and one right maxilla with M^1 and M^2 (HUA-K04136a and b respectively; possibly belonging to the same individual) from Kannondo Cave Site (Holocene horizons; exact horizon unknown).

Diagnosis

Labial anterocone of M^1 reduced and broadly merged with lingual anterocone; posterostyle, metacone and posterior cingulum absent from M^1 and M^2.

Description

M^1 ——

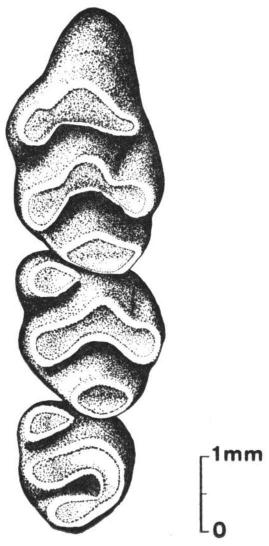

Fig. 198. *Rattus norvegicus*. Occlusal view of the left upper molars from the Holocene horizons of Kannondo Cave Site (HUA-K04136a).

The labial anterocone is considerably reduced in size, and broadly merged with the lingual anterocone, so that the anterior chevron becomes asymmetrical. The hypocone is large, and oval-shaped in occlusal view. The transverse valley between the hypocone and middle chevron shallows at its lingual end. The posterostyle, metacone and posterior cingulum are completely lacking. This tooth is anchored by five roots.

M^2 ——

The labial anterocone is missing. The central transverse valley shallows at its lingual end as in M^1. The hypocone is large, and exhibits an oval occlusal outline. The posterostyle, metacone and posterior cingulum are absent as in M^1. M^2 is anchored by four roots.

M^3 ——

The pattern resembles that of the normal type of *Apodemus* described in the preceding section (Table 88). The labial anterocone is absent. The central transverse valley extends somewhat obliquely to the transverse axis of the crown, and opens lingually. This tooth is anchored by three roots.

Measurements

The measurements of the molars are given as follows:

	M^1		M^2		M^3	
	Length	Width	Length	Width	Length	Width
HUA-K04136a	3.31	1.98	2.17	1.95	1.70	1.58
HUA-K04136b	3.30	2.05	2.19	1.95	—	—

Comparisons and Discussion

The present fossil materials have the reduced labial anterocone in M^1, which is broadly merged with the lingual anterocone. This character is diagnostic for *R. norvegicus*. Moreover they are well coincident with the living *R. norvegicus* in other dental characters and size (Fig. 200). Therefore they are assignable to *R. norvegicus*.

The fossils of *R. norvegicus* are reported from the Late Pleistocene of Shiriya Quarry (KOWALSKI and HASEGAWA, 1976). Although NAORA (1972) disapproved of its geological age, this record is important. This commensal rat seems to be existent since the Late Pleistocene in Japan.

Rattus aff. ***norvegicus*** (BERKENHOUT, 1769)

(Fig. 199)

Materials ——

Locality 4 of Ube Kosan Quarry

5 isolated M^1 (ASM 701993–701997), 7 isolated M^2 (ASM 701998–702004), 4 isolated M_1 (ASM 702005–702008), 10 isolated M_2 (ASM 702009–702018).

Description

The present fossil materials are composed of the isolated molars which are poorly preserved. Their roots and dentine are completely lost.

M^1 ——

The prestyle is absent. The precingulum is usually absent, but rarely observed as a weak cingulum on the antero-buccal face of the crown. The labial anterocone is poorly developed. This cusp is attached on the buccal face of the lingual anterocone and well confluent with the latter cusp even in slightly worn specimens. Consequently the antero-buccal face of the anterior chevron is flattened, and no grooves are found there. The anterostyle is collumnar in three-dimensional shape. It is separated from the lingual anterocone in slightly worn teeth, and situated somewhat posterior to the latter cusp. The middle chevron is composed of three well-developed cusps. The connection of the occlusal surface between the protocone and paracone is earlier than that between the former cusp and enterostyle. The posterostyle and posterior cingulum are completely lacking. The metacone is poorly developed, and forms only a buccal projection of the hypocone. Therefore the posterior chevron shapes a simple and short lamina in slightly worn teeth. As the wear is advanced, its occlusal surface seems to be expanded anteriorly. The two transverse valleys among the anterior, middle and posterior chevrons are considerably deep, so that the occlusal surfaces of these chevrons seem to be hardly confluent with each other even in strongly worn stages.

M^2 ——

The labial anterocone is absent or represented by only a small swelling on the antero-buccal face of the protocone. The other part of the crown is morphologically identical with the corresponding part of M^1.

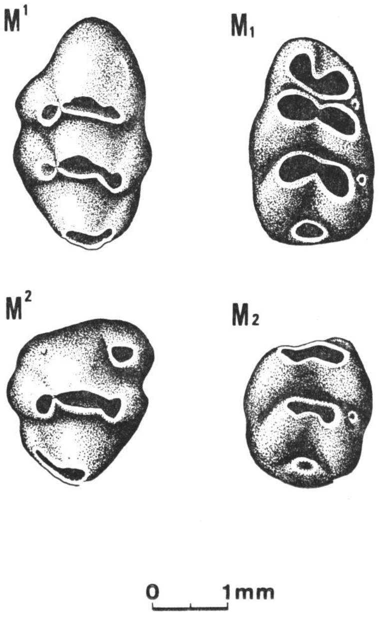

Fig. 199. *Rattus* aff. *norvegicus* from Locality 4 of Ube Kosan Quarry. M^1, ASM 701993 (left); M^2, ASM 702001 (right); M_1, ASM 702007 (right); M_2, ASM 702015 (right).

M_1——

The lingual cusp row is higher than the buccal row. The medial anteroconid is completely lacking, so that the anterior chevron is composed of two cusps such as the lingual anteroconid and labial anteroconid. The former cusp is clearly anterior to the latter. Moreover the former is larger than the latter, although their size difference is variable. These cusps are separated by a longitudinal central groove which opens anteriorly. The angle of the middle chevron is obtuse. The metaconid is larger than the protoconid. In a slightly worn specimen, the middle chevron is clearly divided into these cusps by a narrow central groove, whereas the occlusal surfaces of the entoconid and hypoconid are completely united in the posterior chevron. In another specimen, however, the occlusal surfaces of the cusps of the middle chevron are confluent, while those of the posterior chevron are separated. The transverse valley between the anterior and middle chevrons is narrow and tapers medially. The other transverse valley between the middle and posterior chevrons is much broader.

In most specimens, only one accessory cusp is observable on the buccal face of the hypoconid. This cusp is assigned to C1. It is rather small and round in occlusal view. In one specimen out of four, adding to this cusp, another small cusp (C3) is observed at the buccal entrance of the anterior transverse valley.

M_2——

The width across the anterior chevron is larger than that across the posterior chevron. The lingual cusps are higher than the buccal cusps as in M_1. The angle of each chevron is obtuse. The labial anteroconid is poorly developed and attached

Table 118. Measurements of the molars of *Rattus* aff. *norvegicus* from Locality 4 of Ube Kosan Quarry in mm.

SPECIMEN NUMBER	LENGTH (L)	WIDTH (W)	W / L
M^1			
ASM 701993	2.96	1.81	0.61
ASM 701994	2.83	1.78	0.63
ASM 701995	3.01	1.76	0.59
M^2			
ASM 701998	2.19	1.87	0.86
ASM 701999	2.12	1.74	0.82
ASM 702001	2.20	1.87	0.85
ASM 702002	2.13	1.75	0.82
ASM 702003	2.11	1.69	0.80
M_1			
ASM 702005	2.55	1.60	0.63
ASM 702006	2.71	1.77±	0.66±
ASM 702007	2.70	1.66	0.61
ASM 702008	2.76	1.66	0.60
M_2			
ASM 702009	2.01	1.83	0.91
ASM 702010	2.00	1.80	0.90
ASM 702011	2.04	1.85	0.91
ASM 702014	2.11	1.74	0.83
ASM 702015	2.03	1.68	0.83
ASM 702016	2.00	1.72	0.86
ASM 702017	2.05	1.84	0.90

on the anterior face of the protoconid. The buccal accessory cusp is represented by only one small cusp which is attached on the buccal face of the hypoconid. In one specimen out of eight, another accessory cusp is observed at the lingual entrance of the central transverse valley. It is smaller and lower than the buccal accessory cusp of the same specimen.

Measurements

The measurements of the molars are given in Table 118.

Comparisons and Discussion

The present fossil materials require extensive comparisons with several East and Southeast Asiatic living species, because their geological age is much older than the other fossil materials of *Rattus* described here. The present fossils are considerably different from *R. annandalei* which has abnormal dental characters as *Rattus* (for example, frequent appearance of the posterior cingulum in M^1, and retention of the large labial anterocone in M^2 and M^3). They are also distinguishable from *R. argentiventer*, *R. baluensis*, *R. enganus*, *R. everetti*, *R. exulans*, *R. hoogerwerfi*, *R. losea*, *R.*

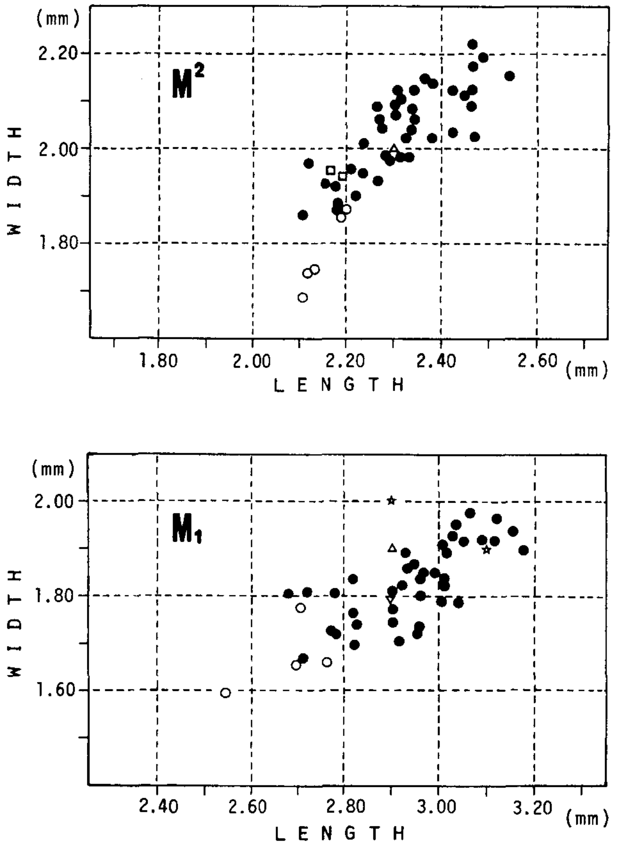

Fig. 200. Length and width plots of M^2 and M_1 of *Rattus* showing the size distribution of the fossil and living specimens from Japan. Open circle, *R.* aff. *norvegicus* from Locality 4 of Ube Kosan Quarry; open square, *R. norvegicus* from Kannondo Cave Site (Holocene horizons); open triangle, *R.* sp. from Ikumo Quarry; open inverted triangle, *R. norvegicus* from Shiriya Quarry; star, *R. norvegicus* or *R. rattus* from Makurazino-ana Cave; solid circle, living *R. norvegicus* from Nagoya (NAKAISHI Collection). The data of Ikumo Quarry, Shiriya Quarry and Makurazino-ana Cave are cited from KOWALSKI and HASEGAWA (1976).

nitidus and *R. rattus* in having more reduced labial anterocone of M^1 which is strongly merged with the lingual anterocone. In regard to this character, the present fossils agree with *R. norvegicus*. However some differences from the latter species are also observed.

Judging from the biometrical data given by HANAMURA *et al.* (1974), the present fossils are smaller than the living *R. norvegicus* from Japan in molar size (especially in width of molars; therefore the present fossils generally have slenderer molars). Moreover the present author examined forty living specimens of *R. norvegicus* collected from Nagoya and obtained the same result (Fig. 200).

MIYAO (1960) analysed the frequency of appearance of the buccal accessory cusps in the lower molars of the living *R. norvegicus* and *R. rattus* collected mainly from Matsumoto. According to him, the frequency of C3 in M_1 is 0% in *R. norvegicus* (number of specimens=41), whereas it is 16.9% in *R. rattus* (number of specimens=42). Subsequently MIYAO *et al.* (1966) examined 224 specimens of the living *R. norvegicus* from various areas of Japan, and reported that C3 is found only in one specimen. In the present fossils, C3 is observed in one specimen out of four. Although the total number of the examined specimens is too scarce, its frequency in the present fossils seems to be higher than that in the living *R. norvegicus.*

The present fossils are too scarce and poorly preserved to decide whether these differences are specific or only intraspecific. Among the above-mentioned species of *Rattus*, however, it can be said that they are most similar to *R. norvegicus.* From this similarity, they are possibly placed in the same lineage as *R. norvegicus*, and thus might be the Middle Pleistocene ancestor of this species.

Rattus sp. from Ikumo Quarry described by KOWALSKI and HASEGAWA (1976) is the only Middle Pleistocene record of *Rattus* other than the present fossils. It is larger than the present fossils (Fig. 200), but has C3 in M_1. The relationship between them is unknown because of the extreme scarcity of the specimens.

Rattus sp.

(Fig. 201)

Materials ——

Kannondo Cave Site (Holocene horizons)
    Horizon C: 2 isolated M^2 (HUA-K04137, 04138).
    Horizon unknown: 1 mandible with I, M_1, M_2 and M_3 (HUA-K04139).
Kitoragawa Site
    1 isolated M_2 (unnumbered)

Description

M^2 ——

The labial anterocone is absent, but a weak cingulum is observed on the antero-buccal face of the crown. The central transverse valley tapers at its lingual end (moreover, in one specimen, it remarkably shallows there). The metacone is recognizable but broadly merged with the large hypocone. The posterostyle and posterior cingulum are completely absent.

This tooth has four roots. In one specimen, an additional rootlet is observed at the posterior face of the antero-buccal root.

Mandible and lower incisor ——

The symphyseal eminence is moderately developed. The angle of diastema (see Fig. 191) is obtuse (about 110°). The lower masseteric crest is well developed. It begins just behind the mental foramen, and extends postero-inferiorly. The

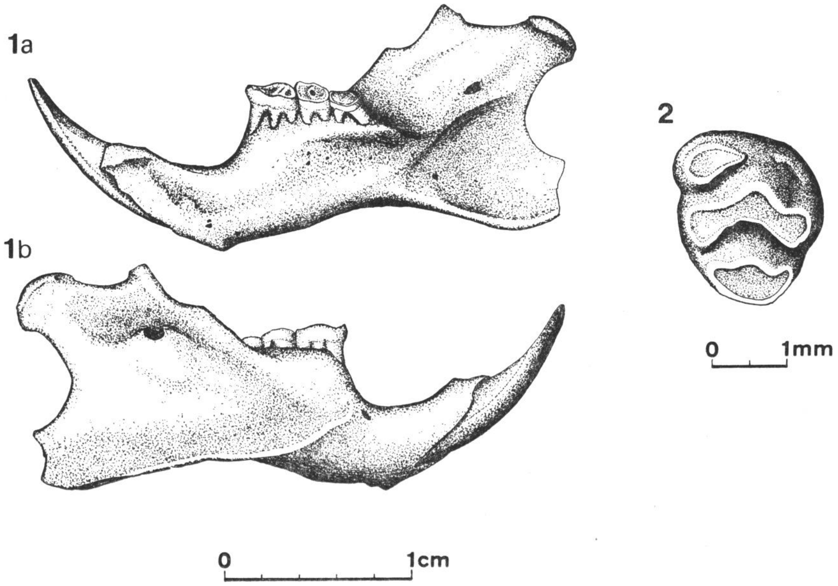

Fig. 201. *Rattus* sp. from Kannondo Cave Site. 1a and 1b, right mandible with I, M_1, M_2 and M_3 from the Holocene horizons (exact horizon unknown, HUA-K04139); 1a, lingual view; 1b, buccal view; 2, occlusal view of the left M^2 from Horizon C (HUA-K04138).

posterior end of the lower incisor forms a prominent tubercle on the buccal face of the ascending ramus. This tubercle is approximately in the same level as the occlusal surfaces of the molars. The mandibular foramen opens near this level at the base of the lingual face of the condylar process.

The lower incisor is normal in shape and has orange colouration on its lower surface.

Lower molars ——

Because the lower molars on the mandible collected from Kannondo Cave Site (HUA-K04139) are strongly worn, the detailed observations of their patterns are impossible. However the number of roots is countable as follows: M_1 with four, M_2 with three and M_3 also with three.

The isolated M_2 from Kitoragawa Site is suitable for observation. It is composed mainly of two chevrons and a large posterior cingulum. The anterior chevron is somewhat straighter than the posterior chevron. In addition to these, a small and low labial anteroconid is present at the antero-buccal corner of the crown, and an accessory cusp is also present at the buccal entrance of the central transverse valley.

Measurements

The measurements of each specimen are given as follows (in mm):

Isolated M^2 from Horizon C of Kannondo Cave Site

	HUA-K04137	HUA-K04138
Length	2.31	2.23
Width	1.99	2.01

Mandible from Kannondo Cave Site (HUA-K04139; the numbers on the left side correspond to those in Fig. 72)

3.	Length from the tip of the incisor to the condyle	29.16
6.	Length of the ascending ramus (the posterior border of M_3 to the condyle)	11.27
8.	Height of the ascending ramus (*gov* to the highest point of the condyle)	11.52
10.	Ditto (*gov* to the mandibular incision)	10.63
12.	Height of the horizontal ramus at M_1	6.00±
13.	Height of the horizontal ramus at M_3	4.74
14.	Maximum thickness of the horizontal ramus	3.20
15.	Length of the molar row (M_1 to M_3) at the crowns	6.34
16.	Ditto at the alveoli	6.64
17.	Length of the molar row (M_1 to M_2) at the crowns	4.52
18.	Ditto at the alveoli	4.55
	Length and width of M_1	2.82; 1.74
	Length and width of M_2	2.04±; 1.85±
	Length and width of M_3	1.93±; 1.50±

Isolated M_2 from Kitoragawa Site

Length ....2.07 Width 1.70

Discussion

These fossil materials are collectively assigned to *Rattus* sp., because they lack diagnostic parts for specific determination. KOWALSKI and HASEGAWA (1976) described some specimens from the Holocene sediments of Makurazino-ana Cave which were assigned to "*R. norvegicus* or *R. rattus*." The present author can not find sufficient reasons in their description why the specimens are exclusively allocated to these two species. He believes that it is better to treat the specimens as *Rattus* sp. as he does.

Family **Gliridae** THOMAS, 1897

Remarks

Small rodents characterized by low-crowned cheek teeth with many transverse ridges are sometimes found in the Japanese Quaternary sediments. They are assignable to Gliridae. In contrast with numerous forms known from the European Neogene and Quaternary, the fossils of the Japanese glirids are referred to a single genus. Recently DAAMS (1981) proposed the subdivision of the family into five subfamilies such as Gliravinae, Glirinae, Dryomyinae, Myomiminae and Graphiurinae, and three genera of *incertae sedis*. He also described the differential characters of these subfamilies. In accordance with his subdivision, the Japanese fossils can be allocated to Dryomyinae in having such characters of cheek teeth as concave occlusal surfaces, complicate patterns with many transverse ridges, main cusps almost indistinguishable from the ridges, complete endoloph in the upper cheek teeth and absence of the longitudinal ridge along the buccal margin of each lower cheek tooth.

DAAMS' Dryomyinae is composed of seven genera such as *Dryomys, Microdyromys, Glirulus, Paraglirulus, Vasseuromys, Bransatoglis* and *Eliomys*. Of these, the taxonomic rank of *Paraglirulus* was reduced to be subgeneric by MEULEN and BRUIJN (1982). In comparison with the dental characters of these genera, the present Japanese fossils are best coincident with *Glirulus*. On the other hand, they can be distinguished from the other five genera by the number and arrangement of the transverse ridges, the continuity of the endoloph in the upper molars and of the endolophid in the lower molars, and the presence or absence of the connection between the anterior centroloph and endoloph in the upper molars. Therefore these Japanese fossils are undoubtedly assigned to *Glirulus*.

Genus *Glirulus* THOMAS, 1905

Remarks

THOMAS (1905b) first proposed the genus *Glirulus* on the basis of the Japanese living species, *G. japonicus*. In 1936, HELLER described *Amphidyromys* as a new genus for the

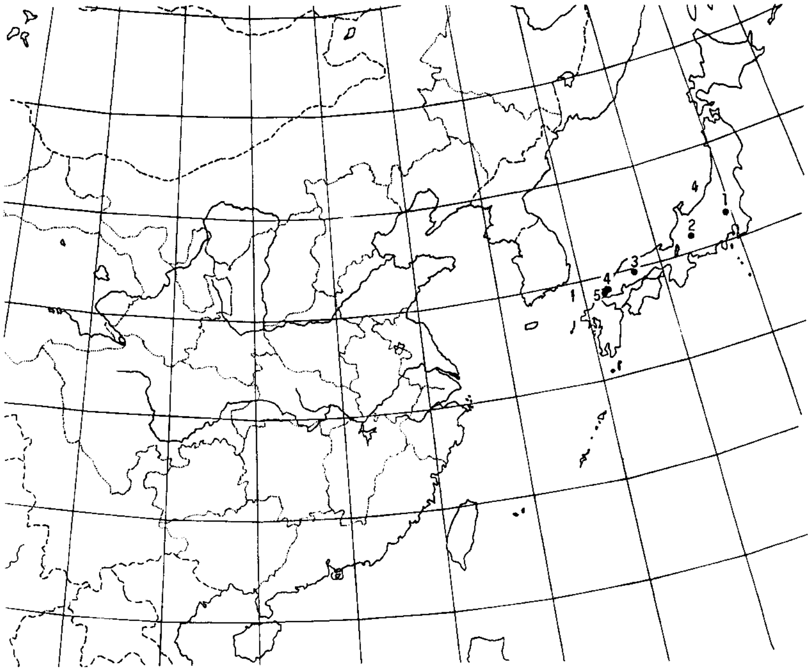

Fig. 202. Fossil localities of *Glirulus* in East Asia (restricted to Japan). 1, Takanosuzawa Cave in the Kuzuü Area; 2, Sugi-ana Cave and Kumaishi-do Cave; 3, Kannondo Cave Site; 4, Ikumo Quarry; 5, Akiyoshi Area (Ando Quarry and Tanuki-ana Cave). For detailed explanation see Table 119.

Table 119. Fossil localities of *Glirulus* in East Asia. The numbers on the left side correspond to those in Fig. 202.

LOCALITY	IDENTIFICATION	REFERENCES
MIDDLE PLEISTOCENE		
4. Ikumo Quarry	*Glirulus japonicus*	Kowalski & Hasegawa (1976)
5. Ando Quarry	*Glirulus japonicus*	Kowalski & Hasegawa (1976)
LATE PLEISTOCENE		
1. Takanosuzawa Cave	*Glirulus japonicus*	Kowalski & Hasegawa (1976)
2. Sugi-ana Cave	*Glirulus japonicus*	Kawamura & Kajiura (1980); this paper
2. Kumaishi-do Cave	*Glirulus japonicus*	Kawamura (1977a); Okumura *et al.*(1982); this paper
3. Kannondo Cave Site (Late Pleist. horizons)	*Glirulus japonicus*	Kawamura (1981); Kawamura *et al.*(1986); this paper
HOLOCENE		
3. Kannondo Cave Site (Holocene horizons)	*Glirulus japonicus*	Kawamura (1978, 1979a); this paper
5. Tanuki-ana Cave	*Glirulus japonicus*	This paper

lower molar obtained from the Pliocene sediments of Germany. Subsequently the close resemblance of *Amphidyromys* to *Glirulus* was properly discussed by KOWALSKI (1963), and he concluded that the former should be included in the latter as a subgenus. However recent authors have treated *Amphidyromys* as a synonym of *Glirulus* (DAAMS 1981, MEULEN and BRUIJN 1982 etc.). According to MEULEN and BRUIJN, two subgenera are recognized in the genus *Glirulus*. They are *Glirulus* THOMAS, 1905 and *Paraglirulus* ENGESSER, 1972. On the other hand, the following species are known as components of the genus:

Glirulus (*Glirulus*) *japonicus* (SCHINZ, 1845)
G. (*G.*) *pusillus* (HELLER, 1936)
G. (*G.*) *lissiensis* HUGUENEY et MEIN, 1965
G. (*G.*) *diremptus* (MAYR, 1979)
G. (*G.*) *conjunctus* (MAYR, 1979)
G. (*Paraglirulus*) *werenfelsi* (ENGESSER, 1972)
G. (*P.*) *agelakisi* MEULEN et BRUIJN, 1982

G. japonicus is an extant species of Japan. The fossils of this species are exclusively known from the Quaternary sediments of Japan (Fig. 202, Table 119). The other six species are all extinct, which are recorded from the Miocene to Early Pleistocene sediments of Europe. On the other hand, any species of *Glirulus* has been hitherto unknown from the continent between these two areas as almost all the other glirids. From palaeobiogeographical viewpoints, such a distribution pattern is quite interesting. It can be interpreted that *Glirulus* had flourished in the Neogene of Europe, and then immigrated to Japan possibly in the Late Pliocene or Early Pleistocene. After this genus was completely extinguished in Europe, it has been able to survive only in Japan. Because *Glirulus* is considered to be an animal which is adapted to temperate forests, the persistence of sylvan environments in Japan throughout the Quaternary possibly permits the survival of this animal.

Glirulus japonicus (SCHINZ, 1845)

(Fig. 203–209)

Myoxus javanicus, SCHINZ 1845, *Syst. Verz. Säug.*, **2,** 230 (subsequently amended as *japonicus* by THOMAS in 1905 who considered the original name as a misprint).

Synonym (*living forms*) ——

Myoxus elegans; TEMMINCK 1844, *Fauna Japonica, Mamm.*, 52–53 (this name was preoccupied by OGILBY, 1838).
Myoxus lasiotis; THOMAS 1880, *Proc. Zool. Soc. London,* **1880,** 40–41.
Glirulus japonicus SCHINZ; THOMAS 1905, *Ibid.*, **1905, 2,** 347–348.
Glirulus japonicus (SCHINZ); KISHIDA 1924, *Honyudobutsu Zukai* (*Monogr. Japanese Mamm.*), 98–102.
Glirulus japonicus (SCHINZ); KURODA 1940, *Monogr. Japanese Mamm.*, 98.
Glirulus japonicus (SCHINZ); IMAIZUMI 1949, *Nat. Hist. Japanese Mamm.*, 231–233.
Glirulus japonicus SCHINZ; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian Mammals,* 542.
Glirulus japonicus SCHINZ; IMAIZUMI 1960, *Coloured Illustr. Mamm. Japan,* 125–126.
Glirulus japonicus; CORBET 1978, *The Mammals of the Palaearctic Region,* 147.

Synonym (*fossil forms*) ——

Glirulus japonicus (SCHINZ); KOWALSKI and HASEGAWA 1976, *Bull. Nat. Sci. Mus.*, Ser. C, **2,** 37; from Ikumo Quarry, Ando Quarry and Takanosuzawa Cave.
Glirulus cf. *japonicus* (SCHINZ); KAWAMURA 1977, *Fossil Club Bull.*, (14), 7; from Kumaishi-do Cave.
Glirulus japonicus (SCHINZ); KAWAMURA 1978, 1979, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre,* **1,** 57; **2,** 46; from the Holocene horizons of Kannondo Cave Site.
Glirulus japonicus (SCHINZ); KAWAMURA and KAJIURA 1980, *Jour. Speleol. Soc. Japan,* **5,** 53; from Sugi-ana Cave.
Glirulus japonicus (SCHINZ); KAWAMURA 1981, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre,* **4,** 69; from the Late Pleistocene horizons of Kannondo Cave Site.
Glirulus cf. *japonicus* (SCHINZ); OKUMURA *et al.* 1982, *Earth Sci.*, **36,** 216; from Kumaishi-do Cave.
Glirulus japonicus (SCHINZ); KAWAMURA *et al.* 1986, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre,* **9,** 71; from the Late Pleistocene horizons of Kannondo Cave Site.

Materials ——

LATE PLEISTOCENE LOCALITIES

Sugi-ana Cave
1 mandible without teeth (KUJC100714)
Kannondo Cave Site (Late Pleistocene horizons; specimen numbers are prefixed by HUA)
Horizon O (lower part): 2 isolated P^4 (K00563, 00564); 1 isolated M^2 (K00565); 1 isolated M_1 (K00566); 2 isolated M_3 (K00567, 00568).

Horizon O (upper part): 1 maxilla without teeth (K00560); 2 mandibles without teeth (K00559, 00561); 1 isolated P_4 (K00558); 1 isolated M_2 (K00562).

Horizon N: 2 isolated P^4 (K00556, 00557); 1 mandible with I (K00553); 1 mandible without teeth (K00554); 1 isolated M_2 (K00552); 1 isolated M_3 (K00555).

Horizon M (lower part): 1 maxilla without teeth (K00550); 1 mandible without teeth (K00551).

Horizon M (upper part): 12 maxillae without teeth (K00362, 00364–00368, 00387–00390, 00392, 00393); 8 isolated P^4 (K00432, 00446, 00465, 00466, 00517, 00530–00532); 28 isolated M^1 (K00373, 00374, 00381, 00405, 00433–00436, 00441–00443, 00447–00449, 00467–00471, 00477, 00518–00522, 00533–00535); 13 isolated M^2 (K00397, 00406–00408, 00430, 00437, 00472–00476, 00536, 00537); 12 isolated M^3 (K00375, 00376, 00438, 00450, 00478–00484, 00539); 4 mandibles with I (K00363, 00394, 00401, 00417); 17 mandibles without teeth (K00369–00372, 00380, 00395, 00396, 00399, 00402–00404, 00418–00421, 00463, 00464); 23 isolated P_4 (K00382, 00409–00411, 00422, 00431, 00439, 00440, 00451–00453, 00485–00491, 00523, 00524, 00540–00542); 29 isolated M_1 (K00377, 00378, 00383, 00384, 00391, 00398, 00400, 00412, 00413, 00416, 00424–00427, 00444, 00454, 00457–00459, 00492–00496, 00525, 00526, 00543–00545); 27 isolated M_2 (K00379, 00385, 00386, 00414, 00415, 00423, 00428, 00429, 00445, 00455, 00456, 00460, 00461, 00497–00508, 00538, 00546); 15 isolated M_3 (K00462, 00509–00516, 00527–00529, 00547–00549).

Kumaishi-do Cave (F_4)

1 isolated M^2 (YKS 00824).

HOLOCENE LOCALITIES

Kannondo Cave Site (Holocene horizons; specimen numbers are prefixed by HUA)

Horizon J: 1 mandible with I (K04140); 1 mandible with M_2 (K04141); 1 isolated M_1 (K04142).

Horizon I: 2 mandibles with I (K04143, 04144); 2 mandibles without teeth (K04145, 04146).

Horizon unknown: 1 mandible with I (K04147).

Tanuki-ana Cave

Layer 4: 1 isolated M^2 (ASM 703367); 1 isolated M_3 (ASM 703368).

Layer 3: 1 isolated M^1 (ASM 703369).

Layer 2: 2 mandibles without teeth (ASM 703370, 703371); 1 isolated M_1 (ASM 703372); 1 isolated M_2 (ASM 703373).

Diagnosis

Size small; maxilla and mandible with 12 and 11 alveolar pits respectively; angular process bent lingually; cheek teeth brachydont; their occlusal surfaces more or less concave; their patterns characterized by many transverse ridges; namely, in general, P^4 and P_4 with 7 ridges, upper molars with 9, and lower molars with 10; endoloph complete in upper cheek teeth; anteroloph, anterior part of the endoloph, protoloph and paracone connecting to each other to form anterior closed loop, while metaloph, posterior part of the endoloph, posteroloph and metacone connecting to form posterior closed loop; third loop usually formed by the connection of the protoloph, anterior centroloph, and central part of the endoloph; lingual face of the upper cheek teeth generally rugose; endolophid usually complete in lower cheek teeth.

Description

Maxilla ——

A weak tubercle is observed immediately posterior to the lower border of the infraorbital foramen. The number of the alveolar pits is 12 (three each for the four teeth). The pits of the lingual row are larger than those of the buccal row. The

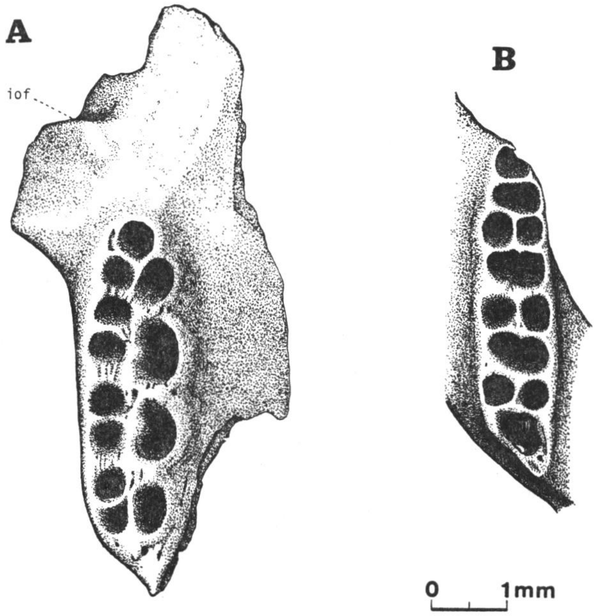

Fig. 203. *Glirulus japonicus*. Alveolar patterns on maxilla (A) and mandible (B). A, right maxilla from the upper part of Horizon M of Kannondo Cave Site (HUA-K00367); B, right mandible from Horizon I of the same site (HUA-K04145); iof, infraorbital foramen.

arrangement of these pits is shown in Fig. 203.

Mandible and lower incisor——

The mental foramen opens immediately anterior to the anterior alveolar pit of P_4. The symphyseal eminence is indistinct. The upper and lower masseteric crests are rather remarkable. The buccal face of the horizontal ramus between these crests is slightly concave. The condyle is not so elevated, and situated at the same level as the lower border of the mandibular incision. The buccal face of the condylar process is widely depressed. The angular process is broad and short. It is strongly bent lingually, but does not extend posteriorly. Its buccal face is slightly depressed immediately above its lower border. The posterior and lower rims of the angular process are remarkably thickened. The lingual face of this process is also broadly concave. The mandibular foramen opens below the posterior margin of the coronoid process. Its position is as high as the level of the alveoli. The area between the alveoli and ascending ramus is narrow and flattened. The number of the alveolar pits is 11 (two for P_4, and three each for the molars). The arrangement of these pits is shown in Fig. 203.

The lower incisor is normal in shape. It resembles those of small murids. The enamel covered surface does not have any grooves and striations.

General characters of the cheek teeth——

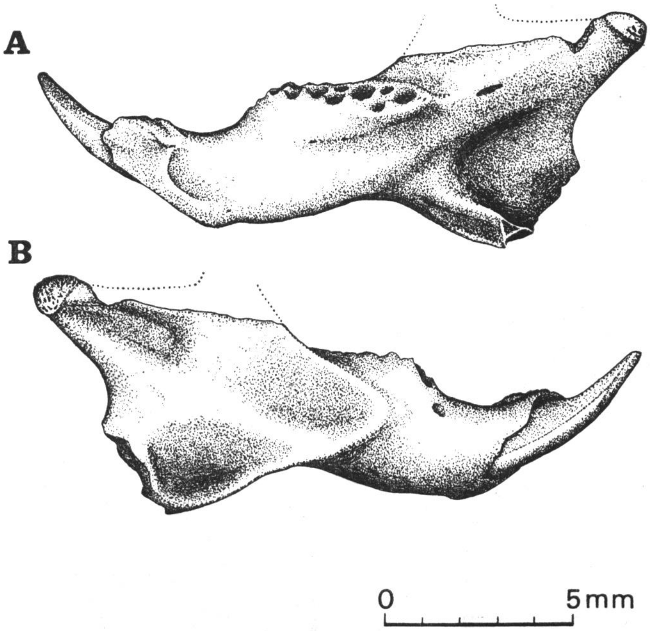

Fig. 204. *Glirulus japonicus.* Right mandible with I from the upper part of Horizon M of Kannondo Cave Site (HUA-K00363). A, lingual view; B, buccal view.

The cheek teeth are extremely low-crowned (Figs. 206, 209). The lingual and buccal margins of the crowns are elevated, while their central parts are longitudinally depressed. The degree of such concavity varies with tooth kind. The occlusal surfaces are rather smoothed, where a number of low transverse ridges are observed. The outlines of the crowns of the upper cheek teeth are broader than long, while those of the lower cheek teeth are longer than broad. Therefore the upper and lower cheek teeth are generally plotted in the areas above and below the line of W (width) =L (length) respectively in the scatter diagrams (Figs. 210, 211). In the upper cheek teeth, the endoloph is almost always complete. However the paracone is separated from the metacone by the central transverse groove. The former cusp is somewhat higher than the latter cusp (1b in Fig. 206). In the lower cheek teeth, the endolophid is usually complete, while the protoconid, mesoconid and hypoconid are almost always separated from each other.

P^4 ——

The outline of the crown is very broadly ovate to depressed ovate. The number of roots is always three. As regards the pattern of the crown and the size, three morphotypes are recognized in the present fossil assemblages. They are Normal Type, and Abnormal Types A and B, as shown in Fig. 207. Normal Type is easily

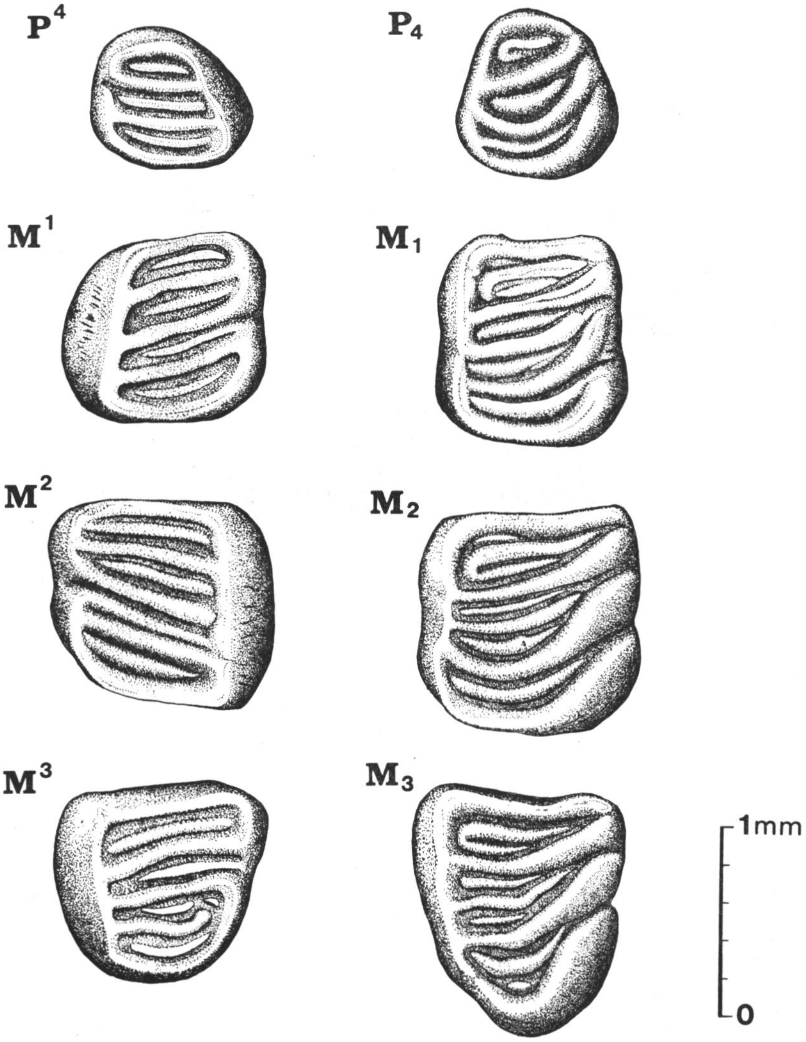

Fig. 205. *Glirulus japonicus*. Occlusal view of the cheek teeth from the upper part of Horizon M of Kannondo Cave Site. M^1 and M^3 are left, while the others are right. P^4, HUA-K00432; M^1, HUA-K00469; M^2, HUA-K00437; M^3, HUA-K00480; P_4, HUA-K00453; M_1, HUA-K00378; M_2, HUA-K00461; M_3, HUA-K00513.

distinguishable from Abnormal Types in having smaller size, seven transverse ridges instead of nine and the anterior root as large as the postero-lingual root. These morphotypes are closely described as follows:

Normal Type (HUA-K00432, 00465, 00466, 00517, 00530–00532, 00556, 00564): The number of the transverse ridges is usually seven; namely four primary

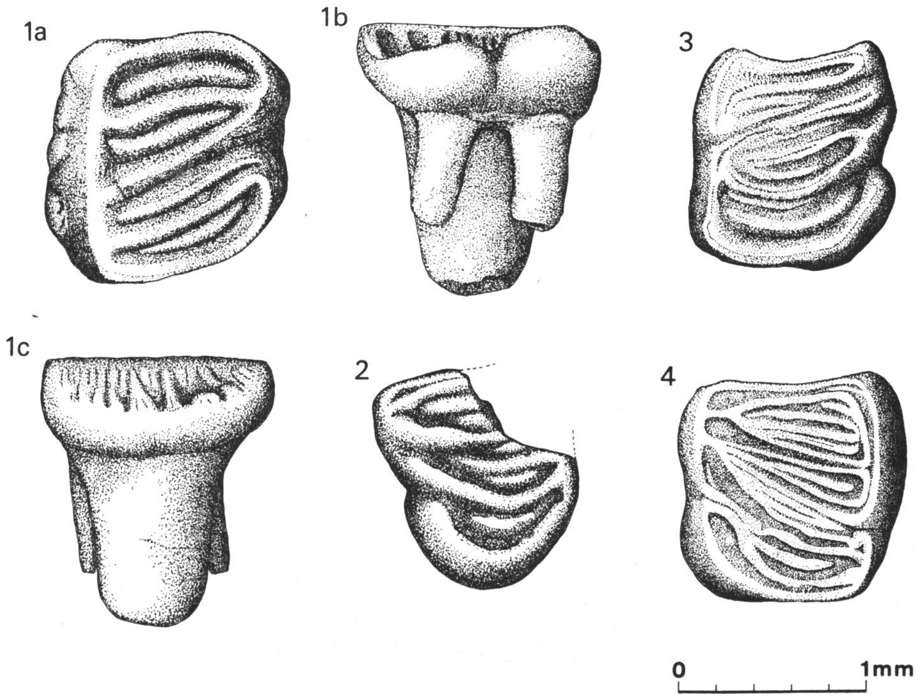

Fig. 206. *Glirulus japonicus*. 1, left M^2 from Kumaishi-do Cave (YKS 00824; 1a, occlusal view; 1b, buccal view; 1c, lingual view); 2, left M_3 from the lower part of Horizon O of Kannondo Cave Site (HUA-K00568); 3, right worn M_1 from Horizon J of Kannondo Cave Site (HUA-K04142); 4, left worn M_2 from the same horizon and site as 3 (HUA-K04141).

ridges (anteroloph, protoloph, metaloph and posteroloph) and three secondary ridges (extra ridge a, anterior centroloph and extra ridge c). In two specimens (HUA-K00531 and 00532) out of nine, however, the number is different. In the former specimen, the extra ridge a is strongly reduced to be a small tubercle, so that the total number becomes six. In the latter, adding to these seven ridges, a weak and short ridge is observed in the buccal part of the valley between the protoloph and anterior centroloph. This additional ridge can be referred to the extra ridge b. It is shorter than the half of the protoloph.

The anteroloph is usually continued to the endoloph. In three specimens (HUA-K00531, 00532 and 00556) out of nine, however, it is slightly separated from the endoloph. The extra ridge a is usually well-developed (in seven specimens out of nine), but reduced to be a short ridge biassed lingually in one specimen (HUA-K00530). Moreover it becomes a small tubercle in another specimen (HUA-K00531) as stated above. The lingual end of the extra ridge a is always separated from the anteroloph. Its buccal end is also separated from the paracone in most specimens, but connected with the cusp in two specimens (HUA-K00466 and 00517) out of nine. The protoloph is always connected with the endoloph and paracone at its lingual and buccal ends respectively. The paracone is mostly separated from the metacone by the central valley between the protoloph and anterior centroloph, or by that between the latter and metaloph, or by both of them. In only one specimen (HUA-K00465) out of nine, however, these cusps are connected by a longitudinal ridge.

The anterior centroloph is nearly as long as the protoloph. Its buccal end is connected to the paracone in two specimens out of nine, and to the metacone in three specimens. In the other four specimens, it is separated from both of them. On the other hand, the lingual end of this loph is never connected to the endoloph. The metaloph, metacone, posteroloph and the posterior part of the endoloph are always connected to each other to form the posterior closed loop. The extra ridge c is always well-developed, but its lingual and buccal ends are always separated from

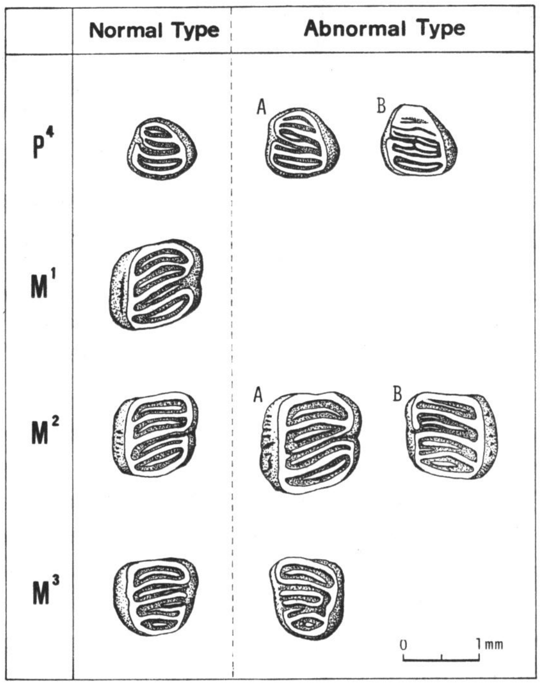

Fig. 207. Morphotypes of the upper cheek teeth of *Glirulus japonicus*. P^4: Normal Type=HUA-K00466, Abnormal Type A=HUA-K00446, Abnormal Type B=HUA-K00557. M^1: Normal Type=HUA-K00447. M^2: Normal Type=HUA-K00536, Abnormal Type A=YKS 00824, Abnormal Type B=HUA-K00537. M^3: Normal Type=HUA-K00481, Abnormal Type=HUA-K00438. All the specimens except YKS 00824 and HUA-K00557 are obtained from the upper part of Horizon M of Kannondo Cave Site. YKS 00824 and HUA-K00557 are from Kumaishi-do Cave and Horizon N of Kannondo Cave Site respectively.

the endoloph and metacone.

The lingual wall of the crown is usually smoothed. In two specimens (HUA-K00432 and 00564) out of nine, however, this wall is slightly ornamented. In one specimen (HUA-K00530), a small additional tubercle is observed on the buccal face of the crown just anterior to the metacone.

The anterior root with a round or transversely elliptic cross section is as large as the postero-lingual root with a round cross section. These roots are clearly larger than the postero-buccal root which is also round in cross section.

Abnormal Type A (HUA-K00446): The outline resembles that of the normal type, but is somewhat elongated anteriorly. Two ridges (extra ridge b and posterior centroloph) are added to the seven ridges usually seen in Normal Type. The anteroloph is continuous to the endoloph. The anterior closed loop is complete. The extra ridge a is well developed, and barely connects to the endoloph and paracone at its lingual and buccal ends respectively. The extra ridge b is short, and biassed buccally. Its buccal end is separated from the paracone. The lingual end of the anterior centroloph is also separated from the endoloph, while its buccal end connects to the paracone. The paracone and metacone are separated from each other by the buccal opening of the valley between the anterior centroloph and posterior centroloph. The posterior centroloph is longer than the extra ridge b, but nearly as long as the half of the metaloph. Its buccal end connects to the metacone. The posterior closed loop is complete as in Normal Type. The lingual end of the extra ridge c is barely connected with the endoloph, but its buccal end is clearly separated from the metacone. The lingual face of the crown is smoothed out without any ornamentation. The anterior root with an elliptical or round cross section is remarkably larger than the postero-lingual root which exceeds the postero-buccal root in size. The cross sections of the last two roots are round.

Abnormal Type B (HUA-K00557): The outline of the crown and the features of the roots are nearly identical with those of Abnormal Type A. The anterior part of the crown is worn out, so that the pattern in front of the protoloph is extinguished (Fig. 207). However eight ridges are observed in the other part of the crown. If the anteroloph and extra ridge a were present in the worn anterior part as in other P^4, the total number of the ridges attains to ten. The extra ridge b is connected with the endoloph, but separated from the paracone. An additional transverse ridge is observed behind the extra ridge b. It is connected with the latter ridge at its buccal end. This additional ridge is nearly as long as the extra ridge b, but much slenderer than the latter. It is slightly interrupted in the middle. The anterior centroloph is also divided into lingual and buccal halves by a central narrow groove. Its buccal end is connected with the metacone. Both ends of the posterior centroloph and extra ridge c are separated from the endoloph and metacone. The posterior closed loop is complete. The lingual wall of the crown is ornamented.

M^1 ——

Because the variation of the pattern is relatively limited, it is not necessary to divide the present fossil assemblages into any morphotype. The outline of the crown is subquadrate. In most specimens, the lingual margin of the crown slightly spreads posteriorly against the buccal margin, so that the width across the posterior part is somewhat larger than that across the anterior part. The lingual face of the crown is usually ornamented. However, such ornamentation is not observed in two specimens (HUA-K00374 and 00471) out of 25.

The number of the transverse ridges is fundamentally nine (namely anteroloph, extra ridge a, protoloph, extra ridge b, anterior centroloph, posterior centroloph, metaloph, extra ridge c and posteroloph). This number is seen in 22 specimens out of 27. In the other five specimens, a few additional ridges are observed. These ridges are always weak and short, and biassed buccally in the valley among the main ridges. In two specimens (HUA-K00435 and 00518) out of these five, an additional ridge is observed in the valley between the metaloph and extra ridge c. It is separated from the metacone. In HUA-K00374, adding to this additional ridge, another supplementary ridge is found in the valley between the protoloph and extra ridge b. It connects to the paracone. On the other hand, the remaining two specimens (HUA-K00448 and ASM 703369) have three additional ridges. They are separated from the adjacent ridges and cusps. In the former specimen, they are found between the protoloph and extra ridge b, between the anterior centroloph and posterior centroloph, and between the posterior centroloph and metaloph. In the latter specimen, they are observed between the protoloph and extra ridge b, between the posterior centroloph and metaloph, and between the metaloph and extra ridge c.

The anterior closed loop is always complete. Both ends of the extra ridge a are usually separated from the paracone and endoloph (in 20 specimens out of 27). In the other seven specimens, its buccal end connects to the paracone or the buccal part of the anteroloph. The central closed loop is also complete in almost all the specimens. In only one specimen (HUA-K00533) out of 27, however, the lingual end of the anterior centroloph is exclusively separated from the endoloph. Both ends of the extra ridge b are usually separated from the paracone and endoloph (in 23 specimens out of 27). In the other three specimens (HUA-K00374, 00534 and ASM 703369), only its buccal end connects to the paracone, while in the remaining one specimen (HUA-K00381), its lingual end exclusively connects to the endoloph. A very small accessory cusp is rarely observed at the buccal opening of the valley between the anterior centroloph and posterior centroloph (in HUA-K00449 and 00470).

The posterior centroloph is almost always well-developed, and nearly as long as the metaloph in most specimens. Its buccal end is usually connected with the metacone (in 22 specimens out of 26). On the other hand, its lingual end is always separated from the endoloph. The posterior closed loop is complete. The extra ridge c is almost always well-developed, but both ends of this ridge are separated from the metacone and endoloph in most specimens. In one specimen (HUA-K00519) out of 27, its buccal end connects to the metacone.

Additional longitudinal ridges are rarely observed in the central part of the crown. They are always short, and never exceed the distance between one transverse ridge and the next one. In HUA-K00521, such a longitudinal ridge branches posteriorly from the buccal part of the protoloph, while another longitudinal ridge connects the anterior centroloph with the posterior centroloph. In HUA-K00477, such a short longitudinal ridge connects the extra ridge b with the anterior centroloph.

M^1 has three roots. The lingual root is much larger than the other two roots. The cross section of the lingual root is narrowly elliptic to crescentic. The buccal face of this root is shallowly grooved in most specimens. The antero-buccal root is as large as, or slightly larger than the postero-buccal root. These buccal roots have round cross sections.

M^2 ——

The outline of the crown is nearly quadrate. The lingual margin is almost parallel to the buccal margin, so that the width across the anterior part is as large as, or slightly larger than that across the posterior part. The postero-buccal corner of the crown curves somewhat more gently than that of M^1. M^2 always has three roots. The features of these roots are identical with those of M^1. As regards the pattern and size, three morphotypes are recognized in the present fossil assemblages. They are Normal Type, Abnormal Types A and B as shown in Fig. 207, which are closely described as follows:

Normal Type (HUA-K00397, 00406–00408, 00430, 00437, 00472–00474, 00536, 00565; ASM 703367): The basic pattern with nine transverse ridges is identical with that of M^1. Additional weak ridges appear only in two specimens (HUA-K00397 and 00430) out of 12. These ridges are always found in the buccal parts of the valleys among the main ridges. Both ends of the ridges are always separated from the main ridges and cusps. In the former specimen, one additional ridge is observed between the extra ridge b and anterior centroloph, and another additional ridge is found between the latter loph and posterior centroloph. In the latter specimen, such a ridge is present between the metaloph and extra ridge c.

The anterior and posterior closed loops are always complete. The central closed loop is also completed in most specimen (9 specimens out of 12). In HUA-K00406 and 00437, however, the lingual end of the anterior centroloph is slightly separated from the endoloph. On the other hand, in HUA-K00397, its lingual end is connected to the endoloph, but its buccal end is separated from the paracone. Both ends of the extra ridge a are almost always separated from the paracone and endoloph (in 11 specimens out of 12). In HUA-K00437, however, its buccal end connects to the paracone. Both ends of the extra ridge b are also separated from the adjacent ridges in almost all the specimens (11 specimens out of 12). But in HUA-K00397, the lingual end of this ridge connects to the endoloph.

The lingual end of the posterior centroloph is always separated from the endoloph, while its buccal end sometimes connects to the metacone (in six specimens out of 12). The extra ridge c is always separated from the endoloph and metacone. The lingual wall of the crown is always ornamented.

Abnormal Type A (YKS 00824): The pattern with nine transverse ridges is included in the variation of Normal Type, but the size is much larger (Figs. 206 and 207). Moreover the ornamentation on the lingual wall of the crown is heavier than that of Normal Type.

Abnormal Type B (HUA-K00537): In addition to the nine ridges generally observed in Normal Type, three short ridges are individually present in the buccal parts of the valleys between the protoloph and extra ridge b, between the extra ridge b and anterior centroloph, and between the posterior centroloph and metaloph (Fig. 207). These ridges are very weak. The anterior closed loop is complete. The buccal end of the extra ridge a barely connects to the buccal part of the anteroloph, while its lingual end is separated from the endoloph. The lingual and buccal ends of the extra ridge b are also separated from the endoloph and paracone respectively. However the lingual and buccal ends of the anterior centroloph connect to the endoloph and metacone respectively. Therefore the anterior centroloph, metacone, metaloph and endoloph form a closed loop which is not equivalent to the central closed loop. Both ends of the posterior centroloph and extra ridge c are separated from the endoloph and metacone. The posterior closed loop is complete. The lingual wall of the crown is ornamented.

M^3 ——

M^3 is divided into two morphotypes such as Normal and Abnormal Types on the basis of the outline and ridge-pattern of the crown (Fig. 207).

Normal Type (HUA-K00375, 00376, 00450, 00478–00483, 00539): The outline is trapezoid with posterior margin somewhat rounded. It is broader than long. The number of the transverse ridges is essentially nine as in M^1 and M^2. This nine-ridged pattern is observed in five specimens out of nine. In the other three specimens, however, the number tends to increase. Namely in HUA-K00376, adding to these nine ridges, a weak and short ridge is observed in the buccal part of the valley between the posterior centroloph and metaloph. In HUA-K00539, there are one additional weak ridge in the buccal part of the valley between the protoloph and extra ridge b, and another weak ridge in that between the latter and anterior centroloph, so that the total number becomes eleven. In HUA-K00481, three additional weak ridges are found individually in the central part of the valleys between the protoloph and extra ridge b, in the buccal part of the valley between the extra ridge b and anterior centroloph, and in the buccal part of the valley between the anterior centroloph and posterior centroloph. On the other hand, in HUA-K00478, the number decreases to be eight, where only two short ridges are present between the protoloph and metaloph.

The anterior closed loop is always complete. The extra ridge a is long, but always separated from the endoloph and paracone. The extra ridge b is well developed in most specimens. Only in one specimen (HUA-K00479) out of ten, however, it is weak, and its length is about the half of the protoloph. The lingual end of the extra ridge b is always separated from the endoloph, while its buccal end connects to the paracone in two specimens (HUA-K00375 and 00376) out of nine. A small tubercle is rarely observed at the buccal opening of the valley between the extra ridge b and anterior centroloph (only in HUA-K00375 out of ten).

The anterior centroloph is nearly as long as the protoloph. Its lingual end connects to the endoloph in most specimens, but is separated from the latter ridge in two specimens (HUA-K00450 and 00539) out of nine. Namely, it connects to the lingual part of the metaloph instead of the endoloph in HUA-K00450, and to that of the extra ridge b in HUA-K00539. The buccal end of the anterior centroloph connects to the metacone in five specimens out of nine, but not in the other specimens.

The posterior centroloph is nearly as long as, or slightly shorter than the metaloph in six specimen out of nine. However it is shorter than the half of the latter ridge in three specimens (HUA-K00450, 00480 and 00482). It is usually separated from the endoloph and metacone (in six specimens out of eight). In HUA-K00481 and 00539, however, it is connected with the metacone only.

The posterior closed loop is almost always complete. In HUA-K00450, however, the lingual end of the metaloph is separated from the endoloph. The extra ridge c is usually well-developed. But it is reduced to be less than or near to the half of the length of the metaloph in two specimens (HUA-K00479 and 00481) out of nine. Its lingual and buccal ends are separated from the endoloph and metacone respectively. The lingual wall of the crown is almost always ornamented (in seven specimens out of eight).

Three roots are observed in most specimens (10 specimens out of 11). The lingual root with a narrowly elliptic cross section is much larger than the antero-buccal and postero-buccal roots. The last two roots have round cross sections, and are usually equal in size. In a few specimens, however, the antero-buccal root is slightly smaller than the postero-buccal one. On the other hand, the lingual and postero-buccal roots are coalescent to form a single root in HUA-K00450, where the total number of roots becomes two. This coalescent root is large, and has an elliptic cross section whose long axis runs obliquely instead of antero-posteriorly. The antero-buccal root is much smaller, and has a round cross section in this specimen.

Abnormal Type (HUA-K00438): The outline is narrowly trapezoid with the posterior margin somewhat rounded. In contrast to Normal Type, it is longer than broad. Therefore this morphotype is plotted below the line of W=L in Fig. 210. Although the number of the transverse ridges is nine as in Normal Type, the ridge pattern is considerably different from that of Normal Type. The anterior closed loop is complete. The extra ridge a is separated from the endoloph and paracone. The lingual ends of the extra ridge b and anterior centroloph are connected with each other, but clearly separated from the endoloph. The posterior centroloph extends lingually from the metacone. This ridge is short, and only as long as the half of the metaloph. A small and low tubercle is observed in the lingual part of the valley between the anterior centroloph and metaloph. The posterior closed loop is complete. The extra ridge c is poorly developed, and composed of two small tubercles which almost contact with each other. The ornamentation on the lingual wall of the crown is absent.

Although the postero-buccal root is broken in HUA-K00438, this morphotype undoubtedly has three roots as Normal Type. The features of the lingual and antero-buccal roots are identical with those of the three-rooted variant of Normal Type.

P_4 ——

The outline of the crown is ovate. The occlusal surface is only slightly concave, and flatter than in the other cheek teeth. The tooth always has two root with nearly the same thickness. The anterior root is usually longer than the posterior one. In two specimens (HUA-K00452 and 00453) out of 24, however, the former is as long as the latter. The cross section of the anterior root is broadly elliptic. The posterior root also has an elliptic cross section, but it is more transversely elongated. P_4 is rather variable in tooth pattern. The following five morphotypes are recognized in the present fossil assemblages:

Normal Type (HUA-K00382, 00409, 00411, 00422, 00439, 00440, 00451–00453, 00485, 00488–00491, 00523, 00524, 00540–00542, 00558): The number of the transverse ridges is fundamentally seven; namely anterolophid, anterior extra ridge, metalophid, centrolophid, mesolophid, posterior extra ridge and posterolophid. In addition to these main ridges, one or two minor extra ridges are often observed. They are weak, and usually shorter than the half of the adjacent main ridges. They generally appear in the lingual part of the valleys among the main ridges. In HUA-K00439, 00440, 00452, 00453, 00524 and 00542, one minor extra ridge is present between the anterior extra ridge and metalophid (minor extra ridge 5 in this case), or between the metalophid and centrolophid (minor extra ridge 4 in this case), or between the centrolophid and mesolophid (minor extra ridge 3 in this case). On the other hand, two minor extra ridges are present in HUA-K00382, 00451, 00485, 00488, 00490 and 00558. These two ridges are assigned to the minor extra ridges 5 and 3 in HUA-K00490, but to the minor extra ridges 4 and 3 in the other five specimens. These minor extra ridges are usually separated from the adjacent ridges, but rarely connected to the endolophid or centrolophid at their lingual ends. Exceptionally, in HUA-K00382, the buccal end of the minor extra ridge 3 is connected to the centrolophid, but its lingual end is separated from the endolophid. On the other hand, the lingual end of the minor extra ridge 5 is connected to that of the anterior extra ridge in HUA-K00453.

The anterolophid and metalophid are connected with the protoconid and metaconid to form an anterior closed loop in nine specimens out of 18. In the other specimens, this loop is left incomplete. Namely it is interruped between the buccal end of the anterolophid and the protoconid in five specimens, and between the lingual end of the metalophid and the metaconid in one specimen. Moreover it is interrupted at both of these positions in the remaining three specimens. The anterior extra ridge is usually separated from the surrounding ridges (in 12 specimens out of 18). However it is connected with the metaconid in three specimens, with the buccal

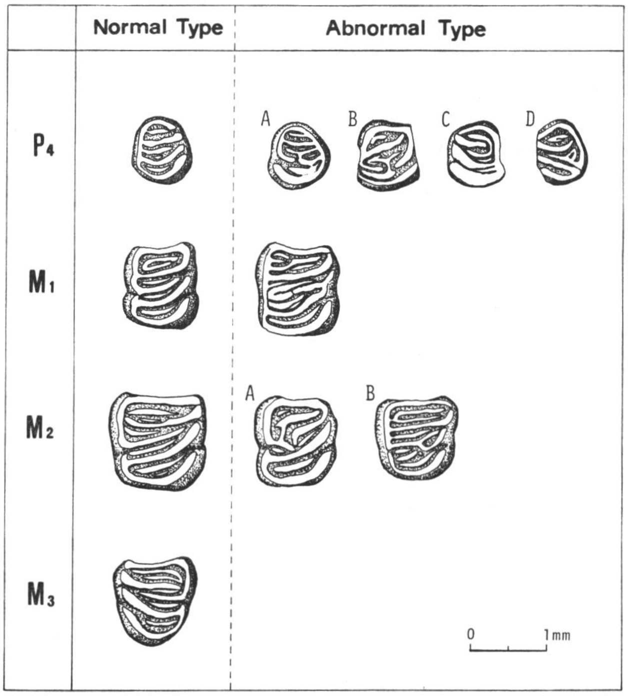

Fig. 208. Morphotypes of the lower cheek teeth of *Glirulus japonicus*. P_4: Normal Type=HUA-K00440, Abnormal Type A=HUA-K00410, Abnormal Type B=HUA-K00431, Abnormal Type C=HUA-K00486, Abnormal Type D =HUA-K00487. M_1: Normal Type=HUA-K00493, Abnormal Type= HUA-K00495. M_2: Normal Type=HUA-K00499, Abnormal Type A= HUA-K00428, Abnormal Type B=ASM 703373. M_3: Normal Type= HUA-K00529. All the figured specimens except ASM 703373 are obtained from the upper part of Horizon M of Kannondo Cave Site. ASM 703373 is from Layer 2 of Tanuki-ana Cave.

part of the anterolophid in one specimen and with both of them in two specimens.

The endolophid is mostly complete. In two specimens (HUA-K00540 and 00558) out of 19, however, it is interrupted immediately anterior to the lingual end of the metalophid. The centrolophid is almost always well-developed. In HUA-K00411, however, it is weak, and shorter than the half of the mesolophid. The lingual end of the centrolophid is sometimes connected with the endolophid (in seven specimens out of 19), but separated in the other 12 specimens. The mesoconid is almost always separated from the protoconid, but connected with the latter cusp only in HUA-K00409. In HUA-K00540, a small tubercle is observed in the valley between these cusps. The lingual ends of the mesolophid and posterolophid are always connected to the endolophid. The posterior extra ridge is usually well-developed, but in five specimens out of 20, it is reduced to be a short and weak ridge. This extra ridge is almost always separated from the hypoconid and entoconid. In two specimens out of 19, however, it is connected to the latter cusp. The hypoconid is always separated from the mesoconid.

Abnormal Type A (HUA-K00410): Although the posterior part of the crown of this specimen is considerably worn, this morphotype is readily distinguishable from Normal Type by the following characters:

1) The mesolophid is divided into two parts by a central longitudinal groove.
2) Moreover, the buccal end of its lingual part is connected by a short longitudinal ridge with the central part of the centrolophid.

Other than these, the following characters are also observed in the present specimen, but they are also seen in some variants of Normal Type:

The seven transverse ridges generally seen in Normal Type are present. Adding to these, the minor extra ridges 3 and 4 are recognized. These minor extra ridges are short and weak. They are biassed lingually, and separated from the other ridges. The anterior closed loop is complete. The lingual end of the anterior extra ridge is connected to the endolophid, while its buccal end is barely separated from the anterolophid. The protoconid and mesoconid are connected with each other to form a buccal longitudinal ridge. This ridge is well separated from the buccal end of the centrolophid and the hypoconid. The lingual ends of the centrolophid and mesolophid are connected to the endolophid. However the lingual and buccal ends of the posterior extra ridge are separated from the entoconid and hypoconid respectively.

Abnormal Type B (HUA-K00431): The crown of this specimen is considerably worn, and its lingual and buccal margins are somewhat damaged. However, the following differential characters are observable in this specimen as the representative of this morphotype:

1) The mesolophid is divided into the lingual and buccal parts which are remotely separated.
2) The centrolophid is connected by a central longitudinal ridge to the posterior extra ridge.

Other than these, the following characters are also observed in the present specimen, but they are also seen in some variants of Normal Type:

Adding to the seven transverse ridges generally seen in Normal Type, there are two minor extra ridges in the lingual parts of the valleys in front of and behind the centrolophid. They are assigned to the minor extra ridges 4 and 3, which are connected with the lingual end of the centrolophid by the wear of the crown. The buccal end of the metalophid is barely separated from the buccal part of the anterolophid. The lingual and buccal ends of the anterior extra ridge, centrolophid and posterior extra ridge are also separated from the adjacent main ridges.

Abnormal Type C (HUA-K00486): The posterior part of the crown of this specimen is strongly worn. Moreover the lingual margin of the crown is broken. In spite of such poor preservation, the following differential characters are observable:

1) The lingual end of the anterior extra ridge is connected by a longitudinal ridge with the lingual end of the centrolophid. These three ridges are separated from the adjacent ridges.
2) The lingual end of the metalophid is remotely separated from the endolophid.

Other than these, the following characters are observed, which are also seen in some variants of Normal Type:

In addition to the seven ridges generally seen in the Normal Type, the minor extra ridge 3 is present in the lingual part of the valley between the centrolophid and mesolophid. The lingual and buccal ends of this extra ridge are separated from the adjacent ridges.

Abnormal Type D (HUA-K00487): The buccal margin of the crown of this specimen is damaged. However the following differential characters are observed:

1) A short diagonal extra ridge and a short longitudinal extra ridge are present in the centro-lingual part of the crown. These two ridges and the centrolophid are connected with each other to form a small closed loop.
2) The posterior extra ridge is lacking.

In addition to these, the following characters are also observed, which are, however, seen in some variants of Normal Type:

Eight transverse ridges are present. They are assignable to the anterolophid, anterior extra ridge, minor extra ridge 5, metalophid, minor extra ridge 4 (the short diagonal extra ridge mentioned above), centrolophid, mesolophid and posterolophid. The lingual and buccal ends of the anterior extra ridge are separated from the anterolophid, endolophid and metalophid. The buccal end of the minor extra ridge 5 is connected with the anterior extra ridge, while its lingual end is separated from the adjacent ridges. The lingual end of the centrolophid is connected with the endolophid, while its buccal end is separated from the adjacent ridges. The endolophid is slightly interrupted just anterior to the lingual end of the mesolophid.

M_1——

The outline of the crown is broadly oblong. Therefore the length of the crown is larger than its width (Fig. 211). The anterior margin of the crown is somewhat concave in occlusal view. M_1 generally has three roots such as antero-buccal, antero-lingual and posterior roots. The antero-lingual root is as thick as or somewhat thicker than the antero-buccal root. The former root is slightly longer than the latter. These two roots have round cross sections. They are usually well separated from each other. In four specimens out of 32, however, their coalescence is observed in various degrees (Fig. 209). The posterior root is much larger than these anterior

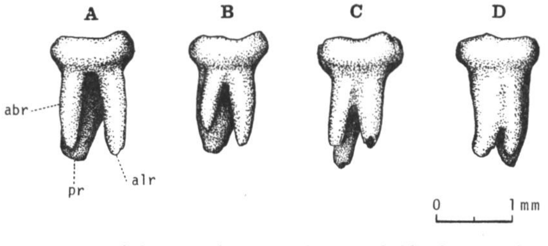

Fig. 209. Coalescence of the anterior roots in M_1 of *Glirulus japonicus*. A, HUA-K00400; B, HUA-K00378; C, HUA-K00427; D, HUA-K00454. abr, antero-buccal root; alr, antero-lingual root; pr, posterior root. All the figures are anterior view. All the figured specimens are collected from the upper part of Horizon M of Kannondo Cave Site.

roots. Its cross section is transversely narrowly elliptic. The anterior face of this root is sometimes shallowly grooved. As regards the pattern of the crown, the following two morphotypes are recognized, which are easily distinguishable from each other by the number of the transverse ridges:

Normal Type (HUA-K00377, 00378, 00383, 00391, 00398, 00400, 00412, 00413, 00416, 00424–00427, 00444, 00454, 00457–00459, 00492–00494, 00496, 00525, 00526, 00543–00545, 00566, 04142; ASM 703372): The basic number of the transverse ridges is ten (Table 120). These ten ridges are composed of seven main ridges (anterolophid, anterior extra ridge, metalophid, centrolophid, mesolophid, posterior extra ridge and posterolophid) and three minor extra ridges. They can be divided into three groups by their lengths. The longest group is composed of the anterolophid, metalophid, mesolophid and posterolophid. The anterior extra ridge, centrolophid and posterior extra ridge comprise the intermediate group. The shortest group is represented by the three minor extra ridges. The lengths of the ridges of the shortest group are generally around the half of those of the longest group.

In addition to these ten ridges, one or two minor extra ridges are sometimes observed. The frequencies of the appearances of the minor extra ridges are given in Table 121. The minor extra ridges 6 and 5 appear in 39.3 and 85.7% of the total specimens respectively, while 4 and 3 are present in all the specimens. On the other hand, the minor extra ridge 2 is found only in 7.1%, and 1 never appears. Of these minor extra ridges, 5, 4 and 3 are well developed, while the others are generally short and weak. These shorter ridges are generally observed in the lingual parts of the valleys among the main ridges. The buccal ends of the minor extra ridges are almost always separated from the adjacent main ridges. Exceptionally, the buccal end of the minor extra ridge 6 is connected to the lingual part of the anterolophid in HUA-K00459, and that of the minor extra ridge 5 is connected to the buccal part of the anterior extra ridge in HUA-K00492. On the other hand, the lingual ends of the minor extra ridges are sometimes connected to the adjacent ridges. Namely the connection of the lingual end of the minor extra ridge 6 with the endolophid is seen in

Table 120. Variation of the number of the transverse ridges in Normal Types of the lower cheek teeth of *Glirulus japonicus*. The number of specimens is given.

	NUMBER OF TRANSVERSE RIDGES							Total Number of Specimens
	7	8	9	10	11	12	13	
P_4	5	5	6	0	0	0	0	16
M_1	0	0	0	20	7	1	0	28
M_2	0	0	1	13	8	1	0	23
M_3	0	0	3	6	1	1	1	12

Table 121. Appearance of the minor extra ridges in Normal Types of the lower molars of *Glirulus japonicus*. The number of the specimens which have each minor extra ridge is shown.

	MINOR EXTRA RIDGE						Number of Examined Specimens
	1	2	3	4	5	6	
M_1	0	2	28	28	24	11	28
M_2	1	1	23	23	22	8	23
M_3	2	1	11	12	11	2	13

two specimens out of 11, while that of the minor extra ridge 5 with the lingual end of the anterior extra ridge is observed in 13 specimens out of 24. The lingual end of the minor extra ridge 4 is connected to the endolophid in two specimens out of 28, and to the lingual end of the centrolophid only in one specimen out of 28. The lingual end of the minor extra ridge 3 is also connected to the endolophid in five specimens out of 28, and to the lingual end of the centrolophid only in two specimens out of 28.

The endolophid is sometimes complete (in 13 specimens out of 27). In the other 13 specimens, however, it is interrupted just anterior to the lingual end of the metalophid, or just anterior to the lingual end of the mesolophid, or at both of these positions. In the remaining one specimen (HUA-K00457), it is interrupted just posterior to the lingual end of the mesolophid. The anterior closed loop is sometimes formed (in 7 specimens out of 28). In the other 21 specimens, it becomes incomplete by the interruptions between the buccal end of the anterolophid and the protoconid (in most specimens) or between the lingual end of the metalophid and the endolophid (only in HUA-K00457). A small tubercle is rarely observed between the anterolophid and minor extra ridge 6 (only in HUA-K00459 out of 11).

The lingual and buccal ends of the anterior extra ridge are usually separated from the adjacent main ridges (23 specimens out of 28). In the other five specimens, its lingual end is connected to the endolophid or the lingual part of the metalophid. The protoconid is always separated from the mesoconid. The lingual end of the centrolophid is usually connected to the endolophid (in 23 specimens out of 29). Its buccal end is usually separated from the protoconid and mesoconid (in 22 specimens out of 28), while it is exclusively connected to the mesoconid in the other six specimens. The lingual end of the mesolophid is usually connected to the endolophid (in 24 specimens out of 28). The mesoconid is almost always separated from the hypoconid (in 27 specimens out of 28). The lingual and buccal ends of the posterior extra ridge are separated from the adjacent ridges in 25 specimens out of 28. Amongst the other three specimens, the connection of its lingual end with the endolophid is observed only in one specimen (ASM 703372), while that of its buccal end with the buccal part of the mesolophid is seen in two specimens (HUA-K00427 and 00526).

Abnormal Type (HUA-K00495): Although the degree of development and the relative lengths of the main transverse ridges are nearly identical with those of Normal Type, this morphotype is easily distinguishable from Normal Type by the following characters:

1) The number of the transverse ridges is 14 (less than 13 in Normal Type).
2) Two minor extra ridges are present in the valley between the anterolophid and anterior extra ridge (unnumbered minor extra ridge and minor extra ridge 6; the former is always absent from Normal Type). These ridges are situated in the lingual part of the valley.
3) A different unnumbered minor extra ridge appears in the lingual part of the valley between the metalophid and minor extra ridge 4 (such a ridge is absent from Normal Type).
4) Another unnumbered minor extra ridge appears in the central part of the valley between the minor extra ridge 3 and mesolophid (such a ridge is also absent from Normal Type).
5) The centrolophid is divided into two parts by a central narrow groove (this ridge is continuous in Normal Type).

In addition to these, the following characters are also observed:

The above-mentioned unnumbered minor extra ridges are generally separated from the adjacent ridges. The lingual ends of the anterolophid, minor extra ridge 6, anterior extra ridge, metalophid, mesolophid and posterolophid are connected with the endolophid, while their buccal ends are separated from each other. The minor extra ridge 5 is present in the central part of the valley between the anterior extra ridge and metalophid. It is separated from the latter two ridges. The lingual end of the minor extra ridge 4 is connected with that of the centrolophid, while both of them are separated from the endolophid. The buccal end of the minor extra ridge 4 is separated from the adjacent ridges, while that of the centrolophid is connected to the mesoconid. The buccal end of the minor extra ridge 3 and both ends of the posterior extra ridge are separated from the adjacent ridges.

M_2 ——

The outline of the crown is quadrate. Therefore the length of the crown approximates its width (Fig. 211). The width aross the anterior part of the crown is nearly equal to or slightly larger than that across the posterior part. The anterior margin of the crown is straight or very slightly concave in occlusal view. M_2 always has three roots. The coalescence of the roots is not observed. The features and relative size of these roots are identical with those of M_1. As regards the pattern of the crown, the following three morphotypes are recognized:

Normal Type (HUA-K00379, 00385, 00414, 00415, 00423, 00429, 00445, 00455, 00456, 00461, 00497–00508, 00546, 00552, 04141): The degree of development, the arrangement and the relative length of each transverse ridge are approximately identical with those of Normal Type of M_1. Moreover the basic number of the transverse ridges is ten as in Normal Type of M_1 (seven main ridges and three minor extra ridges). In addition to these, one or two minor extra ridges sometimes appear. On the other hand, the number of the transverse ridges is rarely reduced to be nine (seven main ridges and two minor extra ridges). Therefore the number varies from nine to twelve (Table 120). The frequencies of the appearances of the minor extra ridges are given in Table 121. The minor extra ridges 6 and 5 appear in 34.8 and 95.7% of the total specimens respectively, while 4 and 3 are seen in all the specimens. The minor extra ridges 2 and 1 appear only in 4.3% each.

The endolophid is complete in 13 specimens out of 21. In seven specimens out of the other eight, it is interrupted just anterior to the lingual end of the mesolophid. In the remaining one specimen (HUA-K00504), it is interrupted at the same position and just posterior to the lingual end of the metalophid. The anterior closed loop is complete only in three specimens out of 21. In 15 specimens out of the other 18, it becomes incomplete by the interruptions between the buccal end of the anterolophid and the protoconid (in 14 specimens) and between the lingual end of the metalophid and the endolophid (in one specimen). In the remaining three specimens, both ends of the metalophid are separated from the endolophid and anterolophid, so that the anterior closed loop is not formed.

The protoconid is always separated from the buccal end of the centrolophid and the mesoconid. The minor extra ridge 6 is always short and weak, when it is present. It appears in the lingual part of the valley between the anterolophid and anterior extra ridge. It is always separated from the adjacent ridges. The buccal end of the anterior extra ridge is always separated from the anterolophid and metalophid, while its lingual end is also separated from the adjacent ridges in 11 specimens out of 21. In 9 specimens out of 21, the lingual end is connected with that of the minor extra ridge 5 but separated from the endolophid. In the remaining one specimen (HUA-K00504), it is connected with the endolophid but separated from the minor extra ridge 5. The buccal end of the minor extra ridge 5 is always separated from the adjacent ridges.

The minor extra ridges 4 and 3 are almost always separated from the adjacent ridges. Exceptionally the former ridge of HUA-K00503 and the latter ridge of HUA-K00504 are connected with the endolophid and mesolophid respectively. The lingual end of the centrolophid is connected to the endolophid in 18 specimens out of 21. Its buccal end is almost always separated from the adjacent ridges, but connected with the mesolophid only in one specimen (HUA-K00415). A small tubercle is observed between the buccal end of the centrolophid and the mesoconid only in HUA-K00546.

The lingual end of the mesolophid is almost always connected to the endolophid. In two specimens (HUA-K00379 and 00504) out of 21, however, it is separated from the endolophid. Both ends of the posterior extra ridge are always separated from the adjacent ridges, while the lingual end of the posterolophid is always connected to the endolophid.

Abnormal Type A (HUA-K00428): This morphotype is considerably different from Normal Type in the following characters:

1) The anterior extra ridge is connected by a longitudinal ridge to the centrolophid, but separated

from the endolophid, anterolophid and metalophid.

2) The metalophid is steeply bent posteriorly at the central part of the crown. However its posterior end is separated from the adjacent ridges.
3) The centrolophid is short and extends postero-buccally.
4) A minor extra ridge between the metalophid and mesolophid is short and weak. It is possibly assigned to the minor extra ridge 4.
5) Another minor extra ridge between the centrolophid and mesolophid is also short and weak. It is possibly assigned to the minor extra ridge 3.

Other than these, the following minor characters are also observed:

In addition to the above-mentioned minor extra ridges, the minor extra ridge 6 is present in the lingual part of the valley between the anterolophid and anterior extra ridge. All of these minor extra ridges are separated from the adjacent ridges. The lingual ends of the anterolophid, centrolophid, mesolophid and posterolophid are connected to the endolophid which is interrupted just posterior to the lingual end of the centrolophid. The lingual and buccal ends of the anterior and posterior extra ridges are separated from the adjacent ridges. The mesoconid is also separated from the protoconid and hypoconid.

Abnormal Type B (ASM 703373): This morphotype remarkably differs from Normal Type in the pattern of the crown posterior to the centrolophid. The differential characters of this morphotype are as follows:

1) The mesolophid seems to be divided into three parts such as a buccal part including the mesoconid, a central small tubercle and a lingual part which is separated from the endolophid.
2) The lingual end of the buccal part of the mesolophid is connected with the central part of the centrolophid instead of the small tubercle and its lingual part.

These characters are never observed in Normal Type and Abnormal Type A. The other characters of the present morphotype are described as follows:

The anterolophid is connected with the endolophid which is slightly interrupted just posterior to the lingual end of the centrolophid. The lingual end of the anterior extra ridge is connected with that of the minor extra ridge 5. The latter is also connected with the endolophid. The buccal ends of the anterolophid, anterior extra ridge, minor extra ridge 5 and metalophid are separated from each other. The lingual ends of the metalophid, minor extra ridge 4 and centrolophid are connected to the endolophid, while their buccal ends are separated from each other. The mesoconid is also separated from the protoconid, hypoconid and the buccal end of the centrolophid. The minor extra ridge 3, the lingual part of the mesolophid and the posterior extra ridge are free from the adjacent ridges. The posterolophid is connected to the endolophid.

M_3——

The outline of the crown is broadly obovate. The anterior margin of the crown is straight or slightly concave in occlusal view. In comparison with the other cheek teeth, the variation of the pattern is rather restricted. Therefore the present fossil assemblages are not divided into any morphotype.

The basic number of the transverse ridges is ten as in Normal Types of M_1 and M_2. These ten ridges are composed of the seven main ridges and three minor extra ridges (minor extra ridges 5, 4 and 3). Such a basic pattern is observed in six specimens out of 12 (Table 120). In the other three specimens, the number of the ridges tends to increase. Namely in HUA-K00528, 11 transverse ridges are observed, which are assigned to the seven main ridges and minor extra ridges 6, 5, 3 and 1. In HUA-K00555, five minor extra ridges (minor extra ridges 6, 5, 4, 3 and 1) are added to the seven main ridges. Moreover in HUA-K00567, the total number attains to 13 (the seven main ridges, and minor extra ridges 5, 4, 2 and 1, and two minor extra ridges between the centrolophid and mesolophid). On the other hand, in the remaining three specimens, the number decreases to be nine. Namely the transverse ridges are represented by the seven main ridges and two minor extra ridges (minor extra ridges 5 and 4 in HUA-K00510 and 00515, but 4 and 3 in HUA-K00516). The frequencies of the appearances of these minor extra ridges are shown in Table 121. The minor extra ridges are generally weak, and appear in the lingual to central parts of the valleys among the main ridges.

The endolophid is complete in four specimens out of 14. In the other specimens, however, it is interrupted just anterior to the lingual end of the mesolophid (in 8 specimens), or just anterior to the lingual end of the centrolophid (in 2 specimens). The buccal end of the anterolophid, the protoconid, the mesoconid and the hypoconid are always separated from each other. The lingual end of the anterolophid is always connected to the endolophid. In case the minor extra ridge 6 is present, it is always separated from the main ridges. The buccal end of the anterior extra ridge is always separated from the adjacent ridges, while its lingual end is connected to the minor extra ridge 5 in five specimens out of 12, to the endolophid in one specimen (HUA-K00462) and to the minor extra ridge 4 in one specimen (HUA-K00516). In the last case, the connection of these two ridges is completed by a short longitudinal ridge which is separated from the endolophid and the lingual end of the metalophid.

The lingual end of the metalophid is sometimes separated from the endolophid (in four specimens out of 14). The buccal end of the minor extra ridge 4 is almost always separated from the adjacent ridges (in 12 specimens out of 13), while its lingual end is also separated from the endolophid in most specimens (11 out of 12). The buccal end of the centrolophid is always separated from the adjacent ridges, while its lingual end is usually connected to the endolophid (in 11 specimens out of 13). Both ends of the minor extra ridge 3 and posterior extra ridge are always separated from the adjacent ridges. The lingual end of the mesolophid is connected to the endolophid in most specimens (14 out of 16). The minor extra ridges 2 and 1 are always separated from the adjacent ridges, when they are present. Only in two specimens (HUA-K00513 and 00515), a small tubercle is observed in the valley between the posterior extra ridge and posterolophid. This tubercle seems to represent an incipient stage of the minor extra ridge 1. The posterolophid is always connected to the endolophid.

M_3 always has three roots. The antero-lingual root is slightly larger than the antero-buccal one. These anterior roots have round cross sections. The posterior root is much larger than the anterior roots. Its cross section is round to broadly

Table 122. Measurements of the mandibles of *Glirulus japonicus* in mm. The numbers on the left side correspond to those in Fig. 72.

	Tanuki-ana Cave	Kannondo Cave Site (Holocene horizons)						
	Layer 2	Horizon unknown	Horizon I				Horizon J	
	ASM 703370	HUA-K 04147	HUA-K 04143	HUA-K 04144	HUA-K 04145	HUA-K 04146	HUA-K 04141	HUA-K 04140
4. Length of the horizontal ramus	–	–	–	7.84	–	–	–	–
5. Length of the diastema	–	–	–	3.80	–	–	–	–
12. Height of the horizontal ramus at P_4	2.50	2.93	2.49	3.17	2.88	–	–	–
13. Minimum height of the horizontal ramus	2.04	2.21	2.06	2.49	2.24	2.61	2.53	2.64
14. Maximum thickness of the horizontal ramus	1.61	1.85	1.69	1.92	1.54	–	–	1.82
16. Length of the cheek tooth row (P_4 to M_3) at the alveoli	–	4.30	4.20	4.16	4.06	4.13±	–	–
18. Length of the molar row (M_1 to M_3) at the alveoli	2.90	3.28	3.24	3.29	3.20	3.16	3.32±	3.26

	Kannondo Cave Site (Late Pleistocene horizons)											Sugi-ana Cave
	Upper part of Horizon M									Horizon N		
	HUA-K 00363	HUA-K 00394	HUA-K 00395	HUA-K 00399	HUA-K 00401	HUA-K 00403	HUA-K 00417	HUA-K 00419	HUA-K 00463	HUA-K 00553	HUA-K 00554	KUJC 100714
4.	–	–	–	–	–	–	–	–	–	–	–	–
5.	–	–	–	–	3.90±	–	–	–	–	–	–	–
12.	3.37	–	3.12	–	3.01	–	3.26±	–	–	–	–	–
13.	2.37	2.16	2.45	2.57	2.47	2.54	2.60	2.15	2.07	2.23	2.50	–
14.	2.09	–	1.73	–	1.98	–	1.64	–	–	–	–	–
16.	4.74±	–	–	–	4.13±	–	–	–	–	4.30±	–	4.01±
18.	3.52	3.09	–	3.31	3.20	–	3.47	3.32±	–	3.14	3.47±	3.06±

elliptic. The coalescence of the roots is not observed.

Measurements

The measurements of the mandibles and cheek teeth are shown in Tables 122–124. The length and width of the cheek teeth are plotted in the scatter diagrams (Figs. 210, 211). These tables and figures indicate that the present fossil cheek teeth have wide ranges of size variation.

Comparisons

Five specimens of the recent *G. japonicus* collected from Nagano Prefecture* are examined for the present comparison. The patterns of the cheek teeth of the present

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* Of these, four specimens belonging to the collection of Aichi-Gakuin University were permitted by the courtesy of H. HANAMURA to examine for the present study.

Table 123. Measurements of the upper cheek teeth of *Glirulus japonicus* in mm.

LOCALITY & SPECIMEN NUMBER	LENGTH	WIDTH
$\underline{P^4}$		
Kannondo Site (Late Pleist. horizons)		
Horizon M (upper part)		
HUA-K00432	0.77	0.87
HUA-K00446	0.92	1.00
HUA-K00465	0.78	0.94
HUA-K00466	0.81	0.94
HUA-K00517	0.84	0.89
HUA-K00530	0.78	0.94
HUA-K00531	0.79	0.96
HUA-K00532	0.83	0.96
Horizon N		
HUA-K00556	0.80	0.85
HUA-K00557	0.96	1.00
Horizon O (lower part)		
HUA-K00564	0.83	1.00
$\underline{M^1}$		
Tanuki-ana Cave (Layer 3)		
ASM 703369	1.19	1.26
Kannondo Site (Late Pleist. horizons)		
Horizon M (upper part)		
HUA-K00374	1.23	1.24
HUA-K00381	1.12	1.28
HUA-K00405	1.08	1.08
HUA-K00433	1.12	1.18
HUA-K00434	1.01	1.10
HUA-K00435	1.17	1.23
HUA-K00436	1.01±	–
HUA-K00441	1.08	–
HUA-K00442	1.18	1.19
HUA-K00443	1.12	1.15
HUA-K00447	1.19	1.19
HUA-K00448	1.16	1.13
HUA-K00449	1.16	1.15
HUA-K00467	1.17	1.14
HUA-K00468	1.17	1.20
HUA-K00469	1.01	1.09
HUA-K00470	1.09	1.21
HUA-K00471	1.07±	1.20±
HUA-K00477	0.98	1.05
HUA-K00518	1.15	1.12
HUA-K00519	1.03	1.04
HUA-K00520	1.02	1.16
HUA-K00521	1.11	1.18
HUA-K00522	1.12	–
HUA-K00533	1.04	1.17
HUA-K00534	1.16	1.24
HUA-K00535	1.10	–
$\underline{M^2}$		
Tanuki-ana Cave (Layer 4)		
ASM 703367	1.01	1.11
Kumaishi-do Cave (F_4)		
YKS 00824	1.36	1.30
Kannondo Site (Late Pleist. horizons)		
Horizon M (upper part)		
HUA-K00397	1.11	1.17
HUA-K00406	1.14	1.21
HUA-K00407	1.09	1.21
HUA-K00408	–	1.15
HUA-K00430	1.16	1.24
HUA-K00437	1.13	1.20
HUA-K00472	1.10	1.19
HUA-K00473	1.20	1.22
HUA-K00474	1.14	1.23
HUA-K00475	1.08±	1.17
HUA-K00536	1.10	1.11
HUA-K00537	1.16	1.18
Horizon O (lower part)		
HUA-K00565	1.15	1.27
$\underline{M^3}$		
Kannondo Site (Late Pleist. horizons)		
Horizon M (upper part)		
HUA-K00375	1.06	1.16
HUA-K00376	1.06	1.20
HUA-K00438	1.06	0.98
HUA-K00450	0.93	1.02
HUA-K00478	0.85	1.02
HUA-K00479	0.91	1.11
HUA-K00480	1.05	1.13
HUA-K00481	0.99	1.09
HUA-K00482	–	1.10
HUA-K00483	0.91	1.02
HUA-K00539	1.00	1.10

fossils are generally well coincident with those of the recent specimens. The variation in the patterns seen in the fossil assemblages is also observed in the recent specimens. Although the present fossils are quite variable in size as mentioned before, the similar size variation is also observed in the recent specimens. For example, YKS 00824 (Abnormal Type A of M^2) is the largest M^2 in the fossil assemblages, while the largest variant in the recent specimens approaches it in size. The similar condition is also observed in the case of smaller specimens. Therefore the present fossils can be identified as *G. japonicus*. Kowalski and Hasegawa (1976) briefly described the fossils of *G. japonicus* from three localities in Japan (Table 119). These fossils are considered

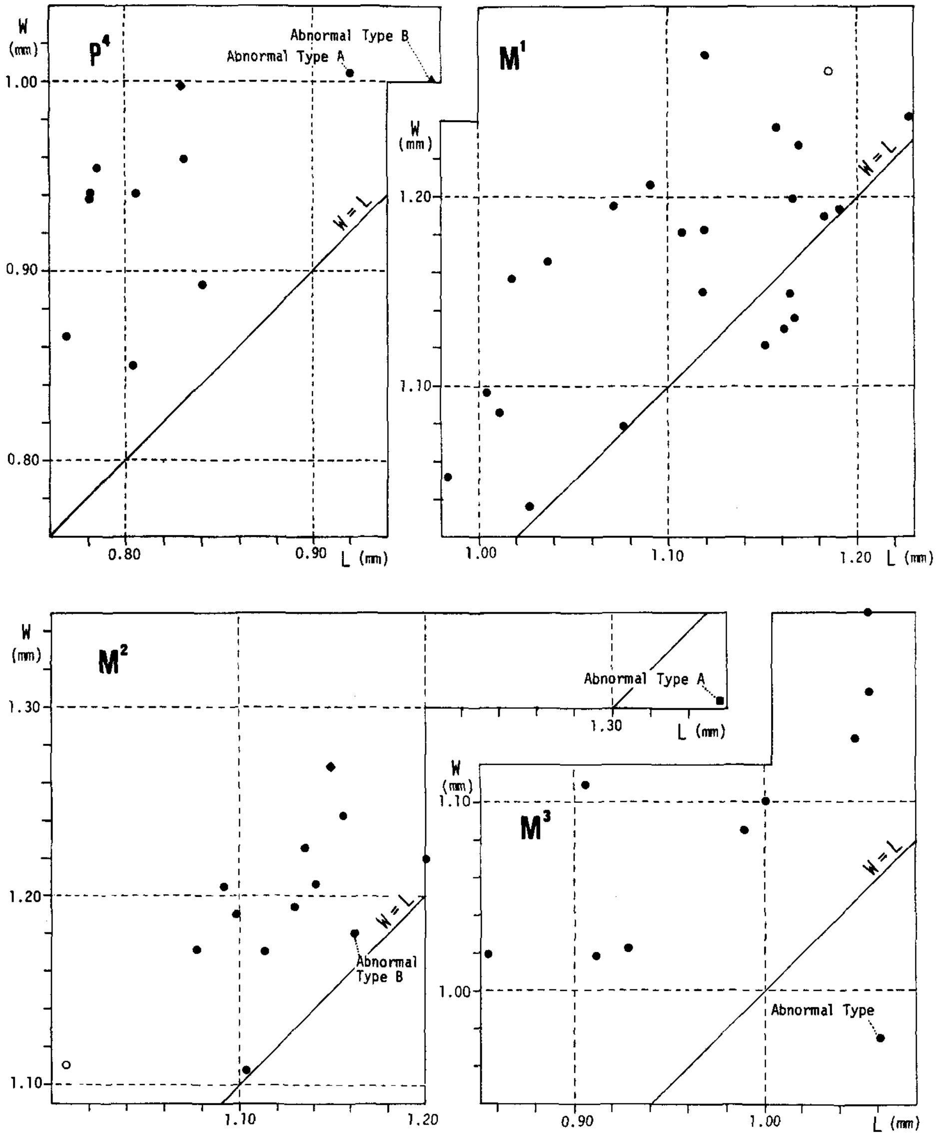

Fig. 210. Scatter diagrams showing the relationship between the length and width of the upper cheek teeth of *Glirulus japonicus*. ◆▲● Late Pleistocene horizons of Kannondo Cave Site (◆ Lower part of Horizon O; ▲ Horizon N; ● Upper part of Horizon M); ■ Kumaishi-do Cave; ○ Tanuki-ana Cave.

to be conspecific with the present fossils from the morphological and biometrical data shown in their paper.

The other six species of *Glirulus* listed before (p. 127) are more or less different

Table 124. Measurements of the lower cheek teeth of *Glirulus japonicus* in mm.

LOCALITY & SPECIMEN NUMBER	LENGTH	WIDTH
$\underline{P_4}$		
Kannondo Site (Late Pleist. horizons)		
Horizon M (upper part)		
HUA-K00382	0.87	0.81
HUA-K00409	0.90	0.84
HUA-K00410	0.88	0.84
HUA-K00411	0.84	0.84
HUA-K00422	0.87	0.82
HUA-K00431	0.95	–
HUA-K00439	0.98	0.86
HUA-K00440	0.88	0.83
HUA-K00451	0.86	0.81
HUA-K00452	0.82±	–
HUA-K00453	0.92	0.87
HUA-K00485	0.92	0.83
HUA-K00486	0.87	–
HUA-K00487	0.87	–
HUA-K00488	0.95	0.86±
HUA-K00489	–	0.82±
HUA-K00490	0.90	0.84
HUA-K00523	0.83	0.71
HUA-K00524	0.93	0.84
HUA-K00540	0.89	0.83
HUA-K00541	–	0.90
HUA-K00542	0.87	0.77
Horizon O (upper part)		
HUA-K00558	1.01	0.90
$\underline{M_1}$		
Tanuki-ana Cave (Layer 2)		
ASM 703372	1.29	1.21
Kannondo Site (Holocene horizon)		
HUA-K04142	1.20	1.08
Kannondo Site (Late Pleist. horizons)		
Horizon M (upper part)		
HUA-K00377	1.22	1.10
HUA-K00378	1.13	1.01
HUA-K00383	1.18	–
HUA-K00384	–	1.02
HUA-K00391	1.15	1.06
HUA-K00398	1.19	1.10
HUA-K00400	1.19	1.07
HUA-K00412	1.10	0.97
HUA-K00413	1.10	1.04
HUA-K00416	1.13	1.07
HUA-K00424	1.10	1.00
HUA-K00425	1.14	1.04
HUA-K00426	1.19	1.03
HUA-K00427	1.25	1.11
HUA-K00444	1.19	1.06
HUA-K00454	1.23	1.06
HUA-K00457	1.17	1.08
HUA-K00458	1.09	1.03
HUA-K00459	1.17	1.09
HUA-K00492	1.13	1.00
HUA-K00493	1.16	0.99
HUA-K00494	1.18	1.07
HUA-K00495	1.20	1.11
HUA-K00525	1.17	1.06
HUA-K00526	1.16	1.05
HUA-K00543	1.14	0.99
HUA-K00544	1.05	1.00
HUA-K00545	1.12	1.04
Horizon O (lower part)		
HUA-K00566	1.20	1.07
$\underline{M_2}$		
Tanuki-ana Cave (Layer 2)		
ASM 703373	1.07	1.08
Kannondo Site (Holocene horizon)		
HUA-K04141	1.18	1.21
Kannondo Site (Late Pleist. horizons)		
Horizon M (upper part)		
HUA-K00379	1.15	1.27
HUA-K00385	1.21	–
HUA-K00414	1.20	1.15
HUA-K00415	1.20	1.17
HUA-K00423	1.05	1.09
HUA-K00428	1.15	1.07
HUA-K00429	1.23±	–
HUA-K00445	1.13	1.15
HUA-K00455	1.12	1.07
HUA-K00456	1.14	1.08
HUA-K00461	1.20	1.20
HUA-K00497	1.15	1.14
HUA-K00498	1.11	1.11
HUA-K00499	1.26	1.28
HUA-K00500	1.25	1.18
HUA-K00501	1.16	1.10
HUA-K00502	1.14	1.14
HUA-K00503	1.20	1.15
HUA-K00504	1.19	1.19
HUA-K00505	1.20	1.11
HUA-K00506	1.13	1.14
HUA-K00507	1.12	1.14
HUA-K00545	1.13	1.13
HUA-K00546	1.09	1.13
Horizon O (upper part)		
HUA-K00562	1.09	1.18
$\underline{M_3}$		
Tanuki-ana Cave (Layer 4)		
ASM 703368	1.09	0.96
Kannondo Site (Late Pleist. horizons)		
Horizon M (upper part)		
HUA-K00462	1.19	1.11
HUA-K00509	1.24	1.09
HUA-K00510	1.16	1.04
HUA-K00513	1.31	1.13
HUA-K00514	1.18	1.02
HUA-K00515	1.17	1.02
HUA-K00516	1.09	1.03
HUA-K00527	1.25	0.97
HUA-K00528	1.24	1.10
HUA-K00529	1.15	1.07
HUA-K00547	1.16	1.10
HUA-K00548	–	1.03
Horizon N		
HUA-K00555	1.30	1.20
Horizon O (lower part)		
HUA-K00567	1.22	1.05

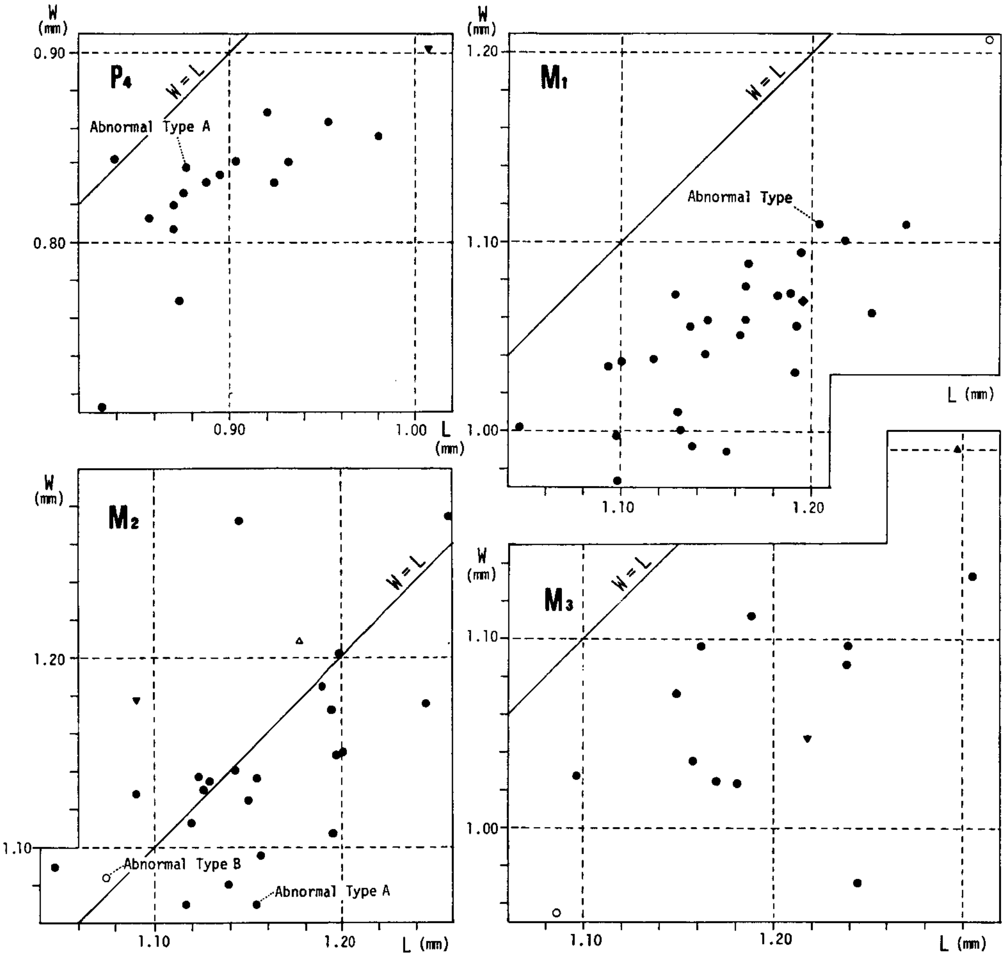

Fig. 211. Scatter diagrams showing the relationship between the length and width of the lower cheek teeth of *Glirulus japonicus*. ◆▼▲● Late Pleistocene horizons of Kannondo Cave Site (◆ Lower part of Horizon O; ▼ Upper part of Horizon O; ▲ Horizon N; ● Upper part of Horizon M); △ Horizon J of Kannondo Cave Site (Holocene); ○ Tanuki-ana Cave

from the present fossils. In accordance with the descriptions and illustrations given by HELLER (1936), DEHM (1962), KOWALSKI (1963), CHALINE (1972) and JÁNOSSY (1972), *G. pusillus* has the following characters in the upper molars (1–4) and lower molars (5):

(1) The endoloph is complete.
(2) The anterior and posterior closed loops are formed.
(3) The anterior centroloph is connected to the endoloph, so that the central closed loop is formed.
(4) The lingual face of the crown is clearly ornamented.
(5) The endolophid is often complete.

These characters are also found in the present fossils. Moreover, the number and arrangement of the transverse ridges of *G. pusillus* is nearly equal to those of the present fossils. Therefore it can be said that *G. pusillus* is quite similar to the present fossils in molar pattern. In spite of these similarities, the molars of *G. pusillus* is significantly smaller than those of the present fossils. Additionally, KOWALSKI (1963) described that M_1 of *G. pusillus* from the Polish Pliocene had two roots, while M_2 from the German Pliocene was said to be three-rooted by HELLER (1936). In the present fossils, however, the lower molars are almost always three-rooted.

In comparison with the descriptions and illustrations of *G. lissiensis* by HUGUENEY and MEIN (1965) and DAXNER-HÖCK and BRUIJN (1981), the following differences are observed between *G. lissiensis* and the present fossils:

(1) *G. lissiensis* is remarkably smaller than the present fossils.
(2) The outline of P^4 is less triangular in *G. lissiensis.*
(3) The number of the transverse ridges of P^4 is nine in *G. lissiensis*, while it is almost always seven in the present fossils.
(4) The anterior centroloph is sometimes separated from, or sometimes connected to the endoloph in the upper molars of *G. lissiensis*, while it is almost always connected to the latter ridge in the present fossils.
(5) The lower molars of *G. lissiensis* have only two roots instead of three.
(6) The endolophid is always interrupted in the lower molars of *G. lissiensis*, while it is often complete in the present fossils.

Because the characters which differentiate *G. conjunctus* from *G. lissiensis* are very slight, MEULEN and BRUIJN (1982) stated that *G. conjunctus* was possibly identical with *G. lissiensis.* Although available data on *G. conjunctus* are quite few in the present study, *G. conjunctus* seems to be different from the present fossils in the same characters as those of *G. lissiensis.*

Judging from the description and illustration given by MEULEN and BRUIJN (1982), *G. diremptus* differs from the present fossils in the following characters:

(1) The size is remarkably smaller.
(2) P^4 has only six transverse ridges (usually seven in the present fossils).
(3) The anterior centroloph is almost always separated from the endoloph in the upper molars (it is almost always connected to the endoloph in the present fossils).
(4) M_1 and M_2 have two roots (almost always three in the present fossils).
(5) The transverse ridges of M_1 and M_2 are slightly fewer.
(6) The endolophid is almost always interrupted in M_1 and M_2 (it is complete in about the half of the present fossils).
(7) The centrolophid is less developed in M_1 and M_2.
(8) The anterior extra ridge, minor extra ridges 4 and 3 are generally less developed in M_3.

Although the cheek teeth of *G. agelakisi* are well coincident with those of the present fossils in size, both of them are quite different in tooth pattern. In accordance with the description and illustrations given by MEULEN and BRUIJN (1982), the differences are as follows:

(1) The ornamentation on the lingual walls of the upper molars is absent or slight in *G. agelakisi*, while it is almost always observed in the present fossils.
(2) P^4 is one-rooted in *G. agelakisi*, while it is always two-rooted in the present fossils.
(3) The patterns of P^4 and M^3 are irregular in *G. agelakisi*. However such irregular patterns are never observed in the present fossils.

(4) The transverse ridges of M^1 and M^2 are more obliquely arranged in the present fossils than in *G. agelakisi.*

(5) The extra ridges a and c of M^1 and M^2 are biassed buccally in *G. agelakisi,* while they are not biassed in the present fossils.

(6) The anteroloph is sometimes separated from the paracone in M^1 and M^2 of *G. agelakisi,* while it is always connected to the latter cusp in those of the present fossils.

(7) The buccal end of the posterior centroloph is rarely connected to the metacone in M^1 and M^2 of *G. agelakisi,* while it is usually connected in the same teeth of the present fossils.

(8) The transverse ridges of M_1 and M_3 are generally fewer in *G. agelakisi* (7 to 10 ridges in M_1, and 7 or 8 in M_3) than in the present fossils (10 and over in M_1, and 9 and over in M_3).

(9) The minor extra ridges 3 and 4 of M_1 are less developed in *G. agelakisi* than in the present fossils.

(10) The metalophid is almost always separated from the metaconid in M_2 of *G. agelakisi,* while the former is almost always connected to the latter in M_2 of the present fossils.

(11) The endolophid of M_2 is always interrupted in *G. agelakisi,* while it is often complete in the present fossils.

Although the morphological data on *G. werenfelsi* are quite inadequately available for the present study, this species seems to be different from the present fossils in the following points:

(1) The anteroloph and anterior centroloph usually end free buccally in this species as in *G. agelakisi,* while these lophs and protoloph are usually connected to each other to form the anterior and central closed loops in the present fossils.

(2) The buccal margins of the upper molars are straight in *G. werenfelsi,* while they are curved inwardly in the present fossils as in *G. agelakisi.*

Summarizing up these comparisons, it is concluded that the present fossils are most similar to *G. pusillus* in the known species of *Glirulus* except *G. japonicus.*

Discussion

The close resemblance of *G. japonicus* to *G. pusillus* is shown in the preceding section. The difference between these two species mainly concerns their size. Considering the chronological ranges of these species, *G. pusillus* is most likely to be the ancestor of *G. japonicus.* Although the morphological difference between *G. pusillus* and *G. lissiensis* is greater than that between *G. pusillus* and *G. japonicus, G. pusillus* was possibly derived from the Miocene species, *G. lissiensis* (Fig. 212). The evolutionary trends in this lineage are represented by the connection of the anterior centroloph with the endoloph in the upper molars, the completion of the endolophid in the lower molars and the increase in number of roots also in the lower molars (from two to three).

In the Late Pliocene or Early Pleistocene, *G. pusillus* or the ancestral form of *G. japonicus* possibly immigrated from Europe to Japan through the temperate forest zone across the Eurasian Continent. The two Japanese endemic insectivore genera such as *Urotrichus* and *Dymecodon* also possibly shifted from Europe in association with *Glirulus.* Soon after this migration, *G. pusillus* seems to have been extinguished from Europe, so that *G. japonicus* became the only representative of *Glirulus.* It is inferred that since this time, *G. japonicus* has inhabited continuously in the forests of Honshu, Shikoku and Kyushu as the above-mentioned insectivores.

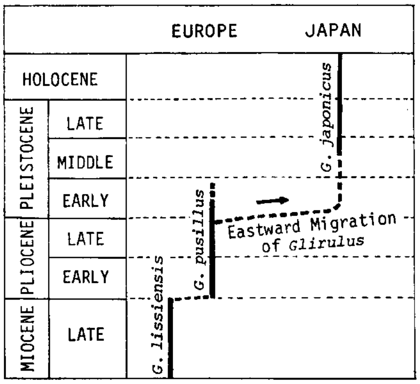

Fig. 212. Tentative phylogeny of *Glirulus japonicus*.

VIII. Faunal Succession

On the basis of the geology and fauna of each fossil locality (in Chapters IV, V and VI) as well as the systematic study of each taxon (Chapter VII), the succession of the rodent fauna in the Japanese Quaternary is explained in this chapter. Before going into the detailed explanation, we should notice that the Japanese Islands are generally divided into the following three biogeographical areas by the recent distribution of mammals.

(a) Hokkaido (including its adjacent small islands).
(b) Honshu, Shikoku and Kyushu (including their adjacent small islands).
(c) Ryukyu Islands.

The boundary between (a) and (b) is drawn in the Tsugaru Strait (BLAKISTON's line), while that between (b) and (c) is present in the Tokara Strait (WATASE's line). Because the remarkable differences in mammalian fauna are nowadays found among these areas, it is assumed that the faunal succession of mammals during the Quaternary has been also considerably different among them. These differences possibly reflect those in geological history among the areas (mainly palaeogeographical conditions). Therefore it is desirable that the faunal succession of rodents is described separately in each area. Unfortunately, owing to the lack of the Pleistocene rodent fossils in (a), the succession of rodent fauna is little known in this area. Therefore the successions in (b) and (c) are exclusively described in the following sentences.

A. Honshu, Shikoku and Kyushu

1. Prior to the middle Middle Pleistocene

Rodent fossils dated as older than the middle Middle Pleistocene are hiterto unknown from this area. However the faunal history of this period can be inferred from the following data:

(1) Fossil records of the middle Middle Pleistocene in this area; especially systematic position and phylogeny of each rodent taxon.

(2) Fossil records prior to the middle Middle Pleistocene in the continent which are summarily given in the descriptions of each genus in Chapter VII.

(3) Distribution and ecology of the continental living species allied to the Japanese species.

The middle Middle Pleistocene rodent fauna is composed mostly of endemic species to this area. However its components can be divided into the following four groups by the homelands of their ancestors inferred from the data of (2) and (3).

Group I: Immigrants from southern Siberia......*Sciurus lis*, *Pteromys momonga*, *Clethrionomys japonicus*.

Group II: Immigrants from northern China......*Microtus epiratticepoides*, *M.* cf. *brandtioides*, *Apodemus speciosus*, *A. argenteus*.

Group III: Immigrant from southern China......*Petaurista leucogenys*.

Group IV: Immigrant from Europe......*Glirulus japonicus*

Although *Cricetulus* sp. and *Myopus schisticolor* appeared transiently in the middle Middle Pleistocene fauna, they are excluded from this grouping.

The ancestors of these grouped forms migrated into this area in the period prior to the middle Middle Pleistocene, and mostly evolved to be the endemic species until the middle Middle Pleistocene. Such speciation possibly resulted from the adaptation to the temperate forests of this area and the geographical isolation from the continental populations.

The species of Group I were originated from the inhabitants of coniferous or cool-temperate forests, and migrated into this area through Sakhalin and Hokkaido or through the Korean Peninsula. *Sciurus lis* and *Pteromys momonga* are closely related to *S. vulgaris* and *P. volans* respectively, and possibly share their ancestors with the last two species. On the other hand, *C. japonicus* was derived from a primitive species of *Clethrionomys* of the Early Pleistocene or Pliocene and evolved along a separated lineage from those of *C. glareolus* and *C. rufocanus* (Fig. 113).

The components of Group II were derived from the inhabitants of the forests or woody grasslands of the cool-temperate zone. They possibly invaded this area through the Korean Peninsula. *Microtus epiratticepoides* possibly arose from the common ancestor to *M. epiratticeps* of northern China in the early Middle Pleistocene. On the other hand, *M.* cf. *brandtioides* which is closely related to *M. brandtioides* of northern China possibly migrated into Japan in association with *M. epiratticepoides* or its ancestor. *Apodemus speciosus* and *A. argenteus* were possibly originated from primitive species of *Apodemus* in the Early Pleistocene, and evolved along two different lineages.

The species of Group III was derived from the ancestor which inhabited in warm-temperate to subtropical forests. If the insectivores of the middle Middle Pleistocene are grouped in the same manner, *Anourosorex japonicus* is allocated to this group. It is assumed that they migrated from southern China in association with *Stegodon orientalis* in the early Middle Pleistocene. Their migration route presumably run through the land bridge which was formed in the area of the present East China Sea.

Group IV is represented by *Glirulus japonicus* only. However, *Urotrichus talpoides* and *Dymecodon pilirostris* are possibly classified into this group, if the insectivores known from the middle Middle Pleistocene are taken into consideration. *G. japonicus* is closely related to *G. pusillus* known from the Pliocene and Early Pleistocene of Europe. The latter species probably shifted eastward through the temperate forest zone of northern Eurasia in the early part of the Early Pleistocene, and evolved to be *G. japonicus*.

2. Since the middle Middle Pleistocene

Abundant fossil records are available for the reconstruction of the faunal succession during this period. These records provide the characters and details of the succession.

Of the rodents immigrated prior to the middle Middle Pleistocene, the species of sciurids, murids and glirids have survived until the present day without any remarkable modification, whereas those of arvicolids underwent remarkable changes in this period. Namely *Clethrionomys japonicus* rapidly evolved into *Phaulomys*, and *Microtus epiratticepoides* and *M.* cf. *brandtioides* were replaced by *M. montebelli*. On the other hand, the faunal exchange with other areas did not take place in this period except the transient immigrations of *Cricetulus* sp., *Myopus schisticolor* and *Microtus montebelli* from the continent in the middle and late Middle Pleistocene.

In comparison with the conditions in Europe and North America, the faunal changes in this area were not so drastic. This possibly indicates that the fluctuations of climatic and vegetational conditions were not so intense as in Europe and North America, and this area was continuously isolated from the continent and Hokkaido during this period except some short times in the Middle Pleistocene.

On the basis of the subdivision of this period given in Chapter VI, the detailed accounts of the faunal succession are given below.

Middle Middle Pleistocene ——

The rodent fauna of this period is characterized by the predominance of the endemic species which seem to have been well adapted to temperate forests as well as by the absence of the following forms:

1. Genera characteristic to the Early Pleistocene and early Middle Pleistocene (for example, *Mimomys*, *"Allophaiomys,"* *Orientalomys* and *Chardinomys*).
2. Genera found mainly in the arctic zone (for example, *Lemmus* and *Dicrostonyx*).
3. Genera found mainly in steppe or desert (for example, *Myospalax*, *Lagurus*, *Ellobius*, *Gerbillus*, *Dipus* and *Allactaga*). However *Cricetulus* is the only exception.
4. Genera found mainly in the subtropical and tropical zones (for example, *Rhizomys*, *Niviventer*, *Leopoldamys* and *Hystrix*).

As regards sciurids, three species such as *Sciurus lis, Petaurista leucogenys* and *Pteromys momonga* were undoubtedly present in this stage. All of these species are tree and flying squirrels, but ground squirrels including *Tamias, Marmota* and *Spermophilus* are completely absent.

Cricetulus sp., the only representative of cricetids in the Quaternary rodent faunas of Japan, temporally appeared in a relatively dry and cool time of this stage. This form possibly immigrated from the Korean Peninsula, but was soon extinguished with the disappearance of grassland environments.

The arvicolids of this stage were represented by four forms such as *Clethrionomys japonicus, Microtus epiratticepoides, M.* cf. *brandtioides* and *Myopus schisticolor*. The first two predominantly occurred in the rodent fauna, while the last two were rarely found. Especially, *M. schisticolor* transiently immigrated from the northern part of the continent in another cool time of this stage. This species seems to have disappeared soon after its immigration with climatic and vegetational changes.

Three murid forms such as *Apodemus speciosus, A. argenteus* and *Rattus* sp. occurred in this stage. The first two were dominant elements as the above-mentioned two arvicolids. The dominancy of these species has persisted until the present day. On the other hand, *Rattus* sp. rarely occurred in this stage. It might evolve into *R. norvegicus* or its allied form in later stages.

Late Middle Pleistocene ——

The same forms as mentioned in the preceding stage were found in sciurids, murids and glirids. However, remarkable changes took place in the arvicolid fauna. At the beginning of this stage, *Microtus montebelli* first invaded from the Korean Peninsula. This species was the last invader in the rodent fauna of this area. It was possibly derived from *M. arvalis*-like ancestor, and migrated from southern Siberia like the species of Group I mentioned above. After the invasion, this species gradually increased and presumably rivalled the former inhabitants of *Microtus* such as *M. epiratticepoides* and *M.* cf. *brandtioides*. In the early time of this stage, *M. epiratticepoides* was most abundantly found in these three, but then the predominancy was gradually replaced by *M. montebelli*. On the other hand, *M.* cf. *brandtioides* was constantly scarce throughout this stage. At any rate, in contrast with the monospecific condition of the present day, the three forms of *Microtus* were undoubtedly coexistent in this stage. Such a condition persisted until the end of the Late Pleistocene. Because *Microtus* generally inhabits in grasslands to open woodlands of the present Holarctic Region, the coexistence of the three forms probably suggests that the vegetational conditions were somewhat more open in these stages than in the present day.

On the other hand, *Clethrionomys japonicus* also dominated in the rodent fauna. This species presumably started to undergo the evolutionary changes which led it to *Phaulomys* in the later stages (delay of root-formation and change in tooth pattern).

Early Late Pleistocene ——

The faunal composition and relative abundance of sciurids, murids and glirids were unchanged from those of the late Middle Pleistocene. On the other hand, the arvicolid fauna of this stage was considerably different from that of the preceding stage.

Although *Microtus* comprised the three forms as in the late Middle Pleistocene, *M. montebelli* far surpassed the other two forms in abundance which were scarcely found in the rodent fauna of this stage. Moreover *Clethrionomys-Phaulomys* transitional form newly appeared as the result of the evolutionary change of *Clethrionomys japonicus*. This form descended to be *Phaulomys* in the later part of this stage or even in the next stage (Fig. 118).

Late Late Pleistocene ——

No fundamental differences were observed in the faunas of sciurids, murids and glirids between this stage and the early Late Pleistocene. In the arvicolids, however, the following changes were recognized:

Of the three forms of *Microtus*, *M. montebelli* became highly predominant. On the contrary, *M. epiratticepoides* and *M.* cf. *brandtioides* were further diminished, and finally became extinct at the end of this stage, possibly between 15,000 and 10,000 yr. B.P., which was approximately contemporaneous with the time of extinction of several large-mammals including *Palaeoloxodon naumanni* and *Sinomegaceros yabei*. By the acquisition of unrooted molars, *Clethrionomys-Phaulomys* transitional form was completely changed into *Phaulomys* in most areas, which became dominant voles of this stage. Moreover *P. andersoni* and *P. smithii* seem to have already differentiated in this stage.

Several large mammals including *Ursus arctos*, *Alces alces* and *Bison priscus* undoubtedly immigrated from the northern part of the continent in this stage. Therefore it was generally believed that these mammals migrated through the land bridge formed between Honshu and Hokkaido. However no rodent immigrants were recognized in the faunas of the Late Pleistocene. This is also true in other micro-mammals except chiropterans. As already pointed out by KAWAMURA (1985), these facts can be interpreted as assuming the presence of "ice bridge" instead of the land bridge in cold times of this stage. This ice bridge possibly avoided the immigration of the micro-mammals.

Holocene ——

After *Microtus epiratticepoides*, *M.* cf. *brandtioides* and *Clethrionomys-Phaulomys* transitional form disappeared in the ending part of the late Late Pleistocene, the rodent fauna became identical with that of the present day except the presence of *Petaurista* sp. in the early part of this period. This form probably immigrated from southern China in association with *P. leucogenys* in the early Middle Pleistocene, and barely survived until the early part of this period. The time of extinction of this form might be synchronous with that of an exotic carnivore, *Lynx lynx*.

From the later part of the preceding stage to the early part of this stage, *Microtus montebelli* became sparse in west Honshu and Kyushu, and was completely extinguished in Shikoku. These changes presumably resulted from the decrease of grasslands and open woodlands in these areas.

B. Ryukyu Islands

The fossil materials described in Chapter VII were exclusively obtained from the four Late Pleistocene localities such as Minatogawa Site, Gajanbira, Iso and Kuteken. However many previous authors reported rodent fossils from several localities listed in Tables 62, 108, 113 and 116. The fossiliferous sediments of these localities are dated as the Late Pleistocene and Holocene. On the basis of all the fossil records, the succession of the rodent fauna in the islands is considered.

1. Prior to the Late Pleistocene

Because no rodent fossils occur in the sediments prior to the Late Pleistocene, the fauna of this period is little known. The Late Pleistocene rodent faunas of the islands are mostly represented by two murids such as *Tokudaia osimensis* and *Diplothrix legata.* Because these murids are generically endemic to the islands, it is inferred that their speciation took place in some period much earlier than the Late Pleistocene. As already mentioned in Chapter VII, *T. osimensis* was possibly derived from the *Parapodemus-Apodemus* lineage in the Pliocene, but was not related to *Margaretamys beccarii* of Sulawesi. On the other hand, *Diplothrix legata* was probably originated from the primitive murids in the Pliocene or earlier periods which were rather near to *Rattus* than to the lineages of *Lenothrix* and *Lenomys.*

2. Late Pleistocene

In this period, *T. osimensis* was widely distributed in the northern half of the islands, while *D. legata* possibly occupied all the areas of the islands. Other than these dominant species, *Microtus* and *Rattus* seem to have occurred in the restricted areas of the southern part of the islands.

3. Holocene

The distribution areas of *T. osimensis* and *D. legata* were broken into small islands by the rise of sea level, and then these species were extinguished in most islands. Consequently they show relict distribution in the present day. On the other hand, *Microtus* seems to have become extinct before the beginning of this period with the disappearance of its preferable habitats.

IX. Summary

In the Japanese Islands, the geological ages of the Quaternary rodent remains are restricted to the Middle Pleistocene to Holocene. They are mostly found in cave and fissure sediments. In this study, 30 localities which yield rodent remains are examined. The fossiliferous sediments of these localities are described in detail

(in Chapter IV) and their mammalian faunas are numerically analysed (in Chapter V). Moreover a large number of rodent remains obtained from these sediments are systematically described with the analyses of morphological variation and extensive comparisons (Chapter VII).

The geological ages of the sediments are estimated mainly by the non-faunal methods (^{14}C method, U-series method, amino-acid racemization method, fluorine and uranium analyses, tephrochronological and archaeological methods etc.), which are supplemented by the faunal methods (faunal characters of mammals other than rodents; mainly large mammals). On the basis of the results of such age-estimation, the sediments of all the fossil localities are correlated with each other (Fig. 71). Furthermore they are classified into the following five stages (A to E):

A. Holocene......West Fissure of Suse Quarry; Kitoragawa Site; Domen Cave Site; Anagami Rockshelter Site; Holocene horizons of Kannondo Cave Site; Tanuki-ana Cave; Husen-ana Cave; Hirao-ana Cave; Ohera-ana Cave; Ninjinkubo First Cave; Yakubono-ana Cave; Ojika-do Cave; Oiwa-ana Cave; Yoshigatani Third Cave.

B. late Late Pleistocene ......Nojiri-ko Formation; F_8 and F_4 of Kumaishi-do Cave; Sugi-ana Cave (partly); Site 1 (uppermost part only), Sites 2, 4 and 5 of Yage Quarry; East Fissure of Suse Quarry; Late Pleistocene horizons of Kannondo Cave Site; Seiryukutsu Cave; Mejiro-do Cave; Minatogawa Site; Kuteken; Iso; Gajanbira.

C. early Late Pleistocene......Aisawa Quarry; Sugi-ana Cave (mostly); Locality 2 of Ube Kosan Quarry.

D. late Middle Pleistocene......Localities 1, 3 and 4 of Ube Kosan Quarry.

E. middle Middle Pleistocene ......Ikumo Quarry; Sumitomo Quarry; Ando Quarry.

In accordance with such a chronological framework, the faunal successions in the Japanese Islands except Hokkaido are reconstructed.

Honshu, Shikoku and Kyushu ——

In the period prior to the middle Middle Pleistocene, the ancestors of the species found in the later stages immigrated into this area from Europe, southern Siberia, northern China and southern China. Of these, the immigration from Europe seems to be the oldest (probably early part of the Early Pleistocene). After the immigrations, these ancestors mostly evolved to be endemic species to the area. Such evolutionary changes possibly resulted from the adaptation to the temperate forests of the area and the geographical isolation from the continental populations.

Since the middle Middle Pleistocene, the species of sciurids, murids and glirids have survived until the present day without any remarkable modification, whereas those of arvicolids underwent drastic changes. Namely *Myopus schisticolor* appeared in the cool time of the middle Middle Pleistocene, and soon disappeared. *Clethrionomys japonicus* rapidly evolved into *Phaulomys* through the transitional form during the Late Pleistocene. Moreover *Microtus montebelli* immigrated from the continent at the beginning of the late Middle Pleistocene, and then gradually replaced the former inhabitants, *M. epiratticepoides* and *M.* cf. *branditioides*, which were completely extinguished at the end of the Late Pleistocene. In contrast with these families, cricetids transiently appeared in the middle Middle Pleistocene only.

Since the middle Middle Pleistocene, the exchange of the rodent faunas with other areas did not take place except the transient immigrations of *Cricetulus* sp., *Myopus schisticolor* and *Microtus montebelli* in the Middle Pleistocene. This fact indicates that the present area has been mostly isolated from the continent, Hokkaido and the Ryukyu Islands during this period.

Ryukyu Islands ——

The faunal succession in the islands are poorly known in comparison with Honshu, Shikoku and Kyushu. The Late Pleistocene rodent fauna of the islands was represented by two murids such as *Tokudaia osimensis* and *Diplothrix legata* which were generically endemic to the islands. These species were extensively distributed within the islands in the Late Pleistocene, whereas their distribution areas were strongly reduced to be the small areas of the northern part of the islands in the Holocene.

The greater part of the present paper is occupied by the systematic descriptions which provide a base-line of the above-mentioned reconstruction. These descriptions also provide several new ideas concerning the classification, origin and phylogenetic relationship of the Quaternary rodents of Japan. Finally, a brief summary on the descriptions is given in the following sentences:

Sciuridae ——

The remains of sciurids are assigned to *Sciurus lis, Petaurista leucogenys, Petaurista* sp. and *Pteromys momonga*. *S. lis* immigrated from the northern part of the continent in the period prior to the middle Middle Pleistocene. This species was possibly derived from *S. vulgaris* or its ancestral species. *P. leucogenys* is regarded as an immigrant from southern China or Southeast Asia. Its immigration probably took place in association with that of *Stegodon orientalis* in the early part of the Middle Pleistocene. *P.* sp. is an aberrant form known only from the Holocene sediments of Tanuki-ana Cave. *Pteromys momonga* is an immigrant from the northern part of the continent as *S. lis*. This species is closely related to *P. volans*.

Arvicolidae ——

The remains of arvicolids are classified into six forms such as *Clethrionomys japonicus, Clethrionomys-Phaulomys* transitional form, *Phaulomys* cf. *smithii, Microtus montebelli, M. epiratticepoides* and *M.* cf. *brandtioides*. Of these, *C. japonicus* is a new species which is proposed for the remains of red-backed vole from the Middle Pleistocene sediments. This species was possibly derived from the Pliocene or Early Pleistocene species of *Clethrionomys*, and evolved along an independent lineage from *C. rufocanus, C. glareolus* and *C. rutilus*. The ancestor of this species seems to have migrated from southern Siberia. The generic allocation of the two extant red-backed voles such as *smithii* and *andersoni* has been controversial. However this study reveals that these species were derived from *C. japonicus* in Japan, and can be allocated to the endemic genus *Phaulomys*, instead of *Clethrionomys*, *Aschizomys* and *Eothenomys*.

In spite of the classifications by the previous authors, it is concluded that the remains of *Microtus* are assigned to three forms including a new species, *M. epiratticepoides*. This new species possibly shares an ancestor with *M. epiratticeps*, but is remotely related to *M. oeconomus*. Of the remaining two, *M. montebelli* was possibly derived from *M. arvalis* or its Middle Pleistocene ancestoral species. The last form, *M.* cf. *brandtioides* is near to the Chinese fossil species, *M. brandtioides*, but some minor differences are also observed between them. It is inferred that *M. epiratticepoides* and *M.* cf. *brandtioides* are northern China origin, while *M. montebelli* is southern Siberia origin.

Muridae ——

The murid remains are classified into seven forms, namely *Apodemus speciosus*, *A. argenteus*, *Tokudaia osimensis*, *Diplothrix legata*, *Rattus norvegicus*, *R.* aff. *norvegicus* and *R.* sp. *A. speciosus* and *A. argenteus* were probably derived from primitive species of *Apodemus* in the Pliocene and Early Pleistocene of the continent. However various species of *Apodemus* known from the continent never invaded into Honshu, Shikoku and Kyushu since the middle Middle Pleistocene. New ideas are presented to explain the origin and phylogenetic relationship of the two endemic species of the Ryukyu Islands such as *T. osimensis* and *D. legata*. Namely, *T. osimensis* was possibly derived from the *Parapodemus-Apodemus* lineage, but is not related to *Margaretamys beccarii* (=*Rattus beccarii*) of Sulawesi. *D. legata* seems to have evolved along an independent lineage which was far from those of *Lenomys* and *Lenothrix*, but rather near to that of *Rattus*. Although the remains of *Rattus* are rare, its existence in Honshu since the Middle Pleistocene is confirmed.

Gliridae ——

The Gliridae is represented by a single species, *Glirulus japonicus*, in the examined materials. This species is closely related to *G. pusillus* of the Pliocene and Early Pleistocene of Europe. *G. pusillus* probably migrated eastward from Europe to Japan, and then evolved to be *G. japonicus*.

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Plate 1

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

Occlusal view of isolated M^1 showing the ontogenetic change in pattern from the age-classes VI to III-II (for detailed explanation of each age-class see text).

1, 9, 11-21, 25-31, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1,* KUJC96539 from Layer 3; *9,* KUJC96621 from Layer 6; *11,* KUJC96505 from Layer 1; *12,* KUJC96540 from Layer 3; *13,* KUJC96601 from Layer 5; *14,* KUJC96589 from Layer 8; *15,* KUJC96590 from Layer 8; *16,* KUJC96580 from Layer 9; *17,* KUJC96619 from Layer 11; *18,* KUJC96569 from Layer 18; *19,* KUJC96595 from Layer 8; *20,* KUJC96602 from Layer 5; *21,* KUJC96582 from Layer 9; *25,* KUJC96510 from Layer 1; *26,* KUJC96591 from Layer 8; *27,* KUJC96608 from Layer 13; *28,* KUJC96609 from Layer 13; *29,* KUJC96509 from Layer 1; *30,* KUJC96583 from Layer 9; *31,* KUJC96563 from Layer 18).

2, 3, 8, 10, 22, 32-34, 37, *Clethrionomys japonicus* from Locality 1 of Ube Kosan Quarry (*2,* ASM 700106 from Layer 1; *3,* ASM 700060 from Layer 2; *8,* ASM 700056 from Layer 2; *10,* ASM 700045 from Layer 3a; *22,* ASM 700058 from Layer 2; *32,* ASM 700055 from Layer 2; *33,* ASM 700057 from Layer 2; *34,* ASM 700046 from Layer 3b; *37,* ASM 700105 from Layer 1).

4-7, 23, 24, 35, 36, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*4,* KUJC98101; *5,* KUJC98102; *6,* KUJC98109; *7,* KUJC98105; *23,* KUJC98106; *24,* KUJC98110; *35,* KUJC98103; *36,* KUJC98107).

Plate 1

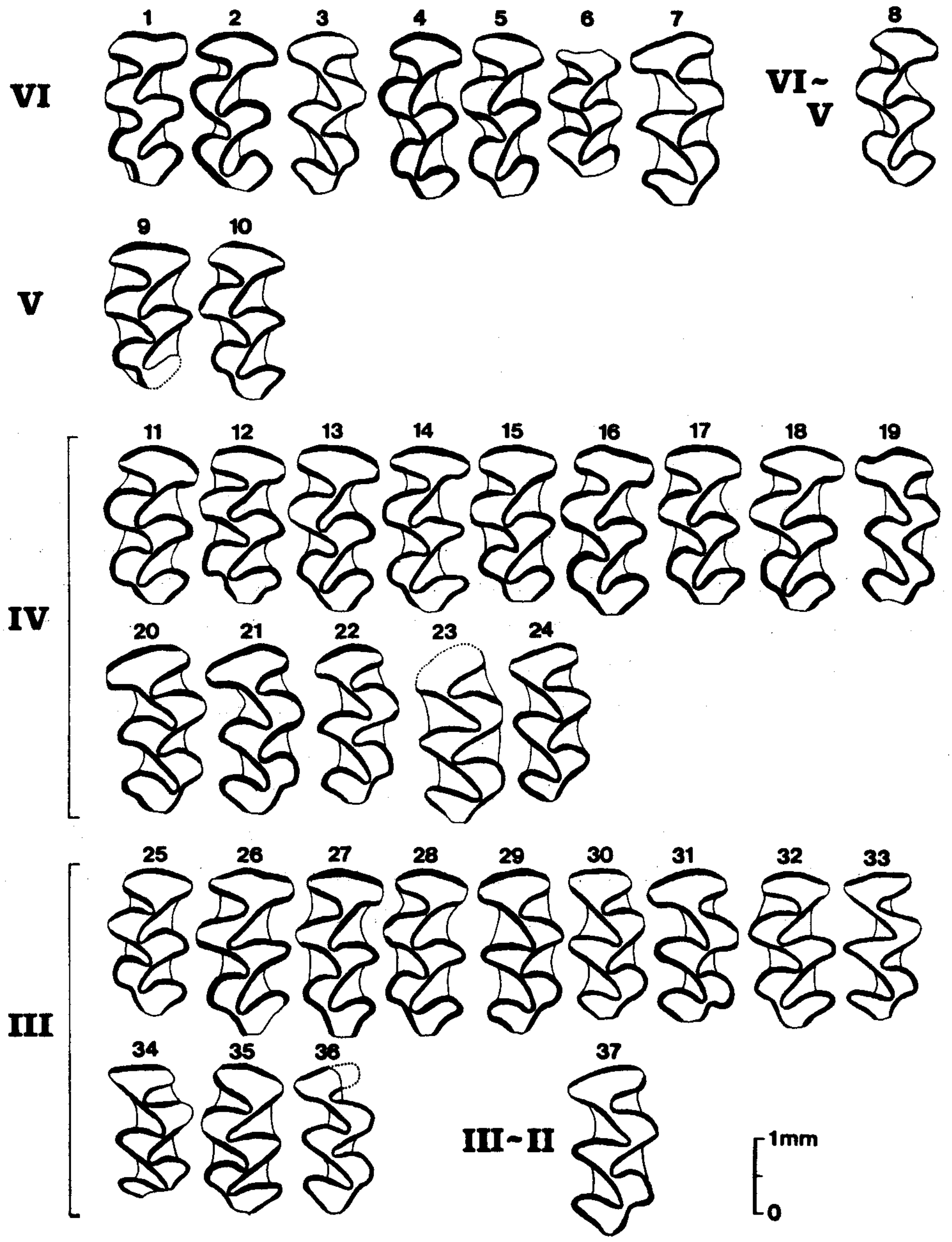
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Plate 2

Clethrionomys japonicus, sp. nov.

Occlusal view of isolated M^1 from Locality 3 of Ube Kosan Quarry, showing the ontogenetic change in pattern from the age-classes II to I.

1, KUJC96506 from Layer 1; *2*, KUJC96570 from Layer 17; *3*, KUJC96536 from Layer 2; *4*, KUJC96603 from Layer 5; *5*, KUJC96511 from Layer 1; *6*, KUJC96553 from Layer 4; *7*, KUJC96615 from Layer 12; *8*, KUJC96610 from Layer 13; *9*, KUJC96611 from Layer 13; *10*, KUJC96625=horizon unknown; *11*, KUJC96520 from Layer 1; *12*, KUJC96522 from Layer 1; *13*, KUJC96535 from Layer 2; *14*, KUJC96544 from Layer 3; *15*, KUJC96545 from Layer 3; *16*, KUJC96584 from Layer 9; *17*, KUJC96614 from Layer 13; *18*, KUJC96604 from Layer 14; *19*, KUJC96507 from Layer 1; *20*, KUJC96512 from Layer 1; *21*, KUJC96513 from Layer 1; *22*, KUJC96514 from Layer 1; *23*, KUJC96521 from Layer 1; *24*, KUJC96526 from Layer 2; *25*, KUJC 96532 from Layer 2; *26*, KUJC96549 from Layer 4; *27*, KUJC96550 from Layer 4; *28*, KUJC96592 from Layer 8; *29*, KUJC96593 from Layer 8; *30*, KUJC96594 from Layer 8; *31*, KUJC96581 from Layer 9; *32*, KUJC96575 from Layer 10; *33*, KUJC96616 from Layer 12; *34*, KUJC96612 from Layer 13; *35*, KUJC96571 from Layer 17; *36*, KUJC96564 from Layer 18; *37*, KUJC96565 from Layer 18; *38*, KUJC96516 from Layer 1; *39*, KUJC96517 from Layer 1; *40*, KUJC96518 from Layer 1; *41*, KUJC96523 from Layer 1; *42*, KUJC96524 from Layer 1; *43*, KUJC96529 from Layer 2; *44*, KUJC96530 from Layer 2; *45*, KUJC96546 from Layer 3.

Plate 2

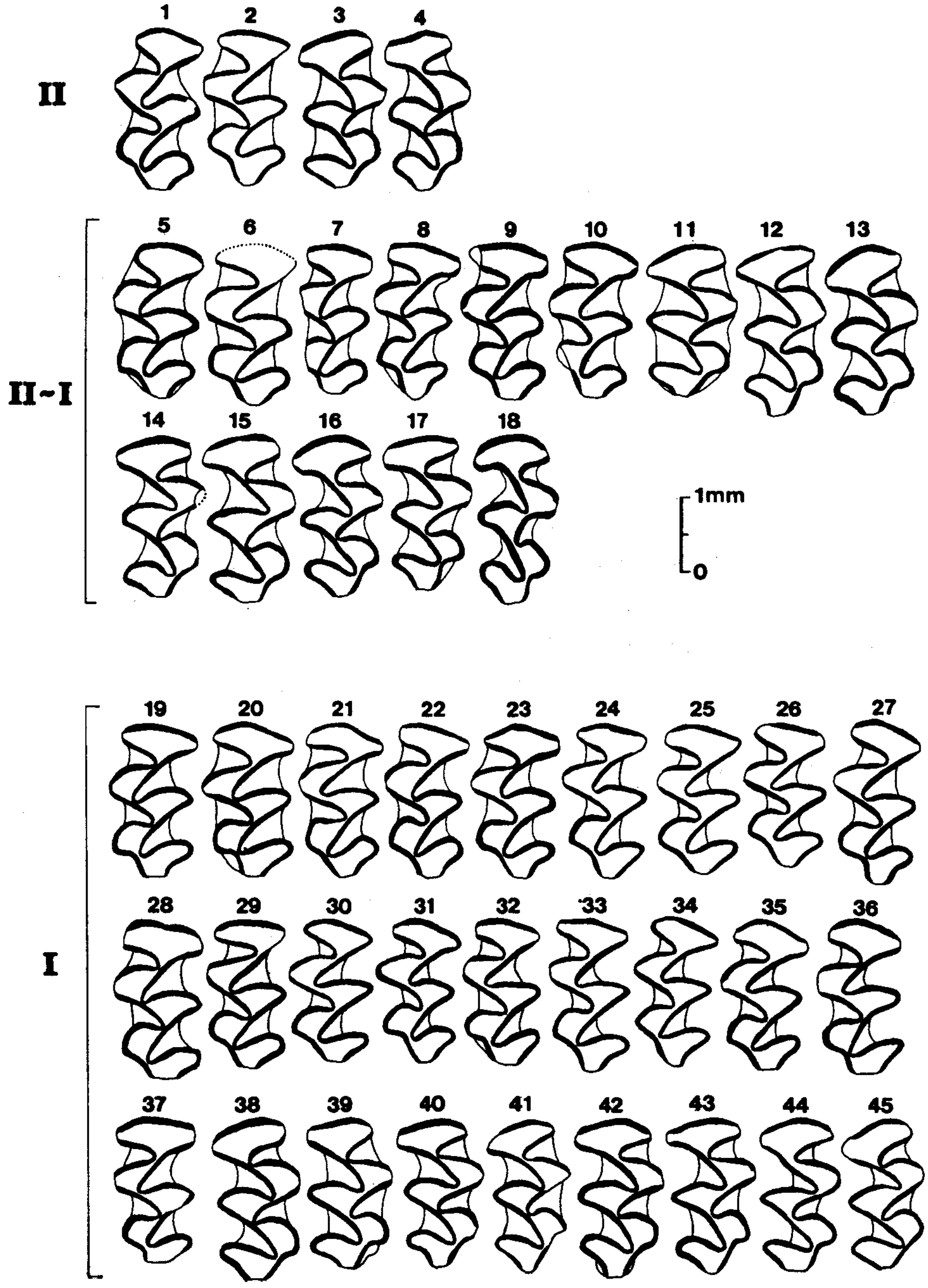
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Plate 3

Clethrionomys japonicus, sp. nov.

Occlusal view of isolated M^1 from Locality 3 of Ube Kosan Quarry, showing the ontogenetic change in pattern from the age-classes I to Y.

1, KUJC96547 from Layer 3; *2*, KUJC96554 from Layer 4; *3*, KUJC96555 from Layer 4; *4*, KUJC96556 from Layer 4; *5*, KUJC96560 from Layer 4; *6*, KUJC96596 from Layer 8; *7*, KUJC 96597 from Layer 8; *8*, KUJC96585 from Layer 9; *9*, KUJC96586 from Layer 9; *10*, KUJC96587 from Layer 9; *11*, KUJC96577 from Layer 10; *12*, KUJC96617 from Layer 12; *13*, KUJC96605 from Layer 14; *14*, KUJC96572 from Layer 17; *15*, KUJC96574 from Layer 17; *16*, KUJC96566 from Layer 18; *17*, KUJC96519 from Layer 1; *18*, KUJC96557 from Layer 4; *19*, KUJC96508 from Layer 1; *20*, KUJC96527 from Layer 2; *21*, KUJC96533 from Layer 2; *22*, KUJC96538 from Layer 2; *23*, KUJC96541 from Layer 3; *24*, KUJC96542 from Layer 3; *25*, KUJC96551 from Layer 4; *26*, KUJC96552 from Layer 4; *27*, KUJC96622 from Layer 6; *28*, KUJC96576 from Layer 10; *29*, KUJC96573 from Layer 17; *30*, KUJC96537 from Layer 2; *31*, KUJC96548 from Layer 3; *32*, KUJC96558 from Layer 4; *33*, KUJC96624 from Layer 6; *34*, KUJC96579 from Layer 10; *35*, KUJC96567 from Layer 18; *36*, KUJC96568 from Layer 18; *37*, KUJC96559 from Layer 4; *38*, KUJC96528 from Layer 2; *39*, KUJC96534 from Layer 2; *40*, KUJC96543 from Layer 3; *41* KUJC 96613 from Layer 13; *42*, KUJC96626=horizon unknown; *43*, KUJC96627=horizon unknown; *44*, KUJC96525 from Layer 1; *45*, KUJC96531 from Layer 2; *46*, KUJC96598 from Layer 8; *47*, KUJC96588 from Layer 9; *48*, KUJC96618 from Layer 12.

Plate 3

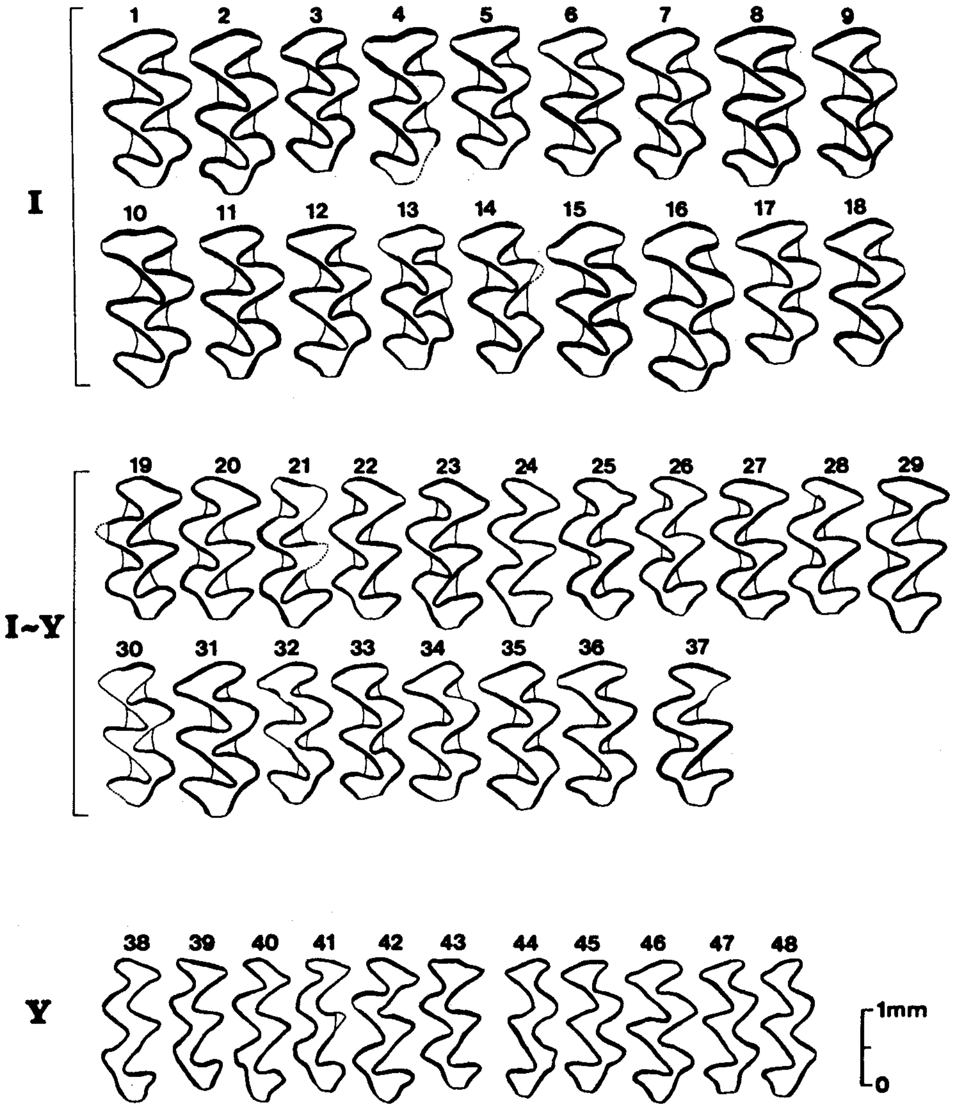
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Plate 4

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

Occlusal view of isolated M^2 showing the ontogenetic change in pattern from the age-classes VI to II-I.

1, 2, 4-6, 9-17, 21-27, 31-35, 37-60, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1,* KUJC96660 from Layer 2; *2,* KUJC96725 from Layer 14; *4,* KUJC96712 from Layer 8; *5,* KUJC96651 from Layer 2; *6,* KUJC96656 from Layer 2; *9,* KUJC96658 from Layer 2; *10,* KUJC 96720 from Layer 5; *11,* KUJC96713 from Layer 8; *12,* KUJC96693 from Layer 10; *13,* KUJC 96728 from Layer 13; *14,* KUJC96674 from Layer 4; *15,* KUJC96697 from Layer 10; *16,* KUJC 96733 from Layer 13; *17,* KUJC14682 from Layer 18; *21,* KUJC96628 from Layer 1; *22,* KUJC 96694 from Layer 10; *23,* KUJC96669 from Layer 4; *24,* KUJC96629 from Layer 1; *25,* KUJC96721 from Layer 5; *26,* KUJC96699 from Layer 10; *27,* KUJC96698 from Layer 10; *31,* KUJC96631 from Layer 1; *32,* KUJC96729 from Layer 13; *33,* KUJC96752=horizon unknown; *34,* KUJC96639 from Layer 1; *35,* KUJC96675 from Layer 4; *37,* KUJC96632 from Layer 1; *38,* KUJC96633 from Layer 1; *39,* KUJC96634 from Layer 1; *40,* KUJC96647 from Layer 1; *41,* KUJC96662 from Layer 3; *42,* KUJC96663 from Layer 3; *43,* KUJC96670 from Layer 4; *44,* KUJC96730 from Layer 13; *45,* KUJC96685 from Layer 18; *46,* KUJC96640 from Layer 1; *47,* KUJC96641 from Layer 1; *48,* KUJC96642 from Layer 1; *49,* KUJC96643 from Layer 1; *50,* KUJC96661 from Layer 2; *51,* KUJC 96665 from Layer 3; *52,* KUJC96666 from Layer 3; *53,* KUJC96744 from Layer 6; *54,* KUJC96745 from Layer 6; *55,* KUJC96746 from Layer 6; *56,* KUJC96734 from Layer 13; *57,* KUJC96705 from Layer 9; *58,* KUJC96706 from Layer 9; *59,* KUJC96726 from Layer 14; *60,* KUJC96687 from Layer 18).

7, 8, 18, *Clethrionomys japonicus* from Layer 2 of Locality 1 of Ube Kosan Quarry (*7,* ASM 700066; *8,* ASM 700063; *18,* ASM 700062).

3, 19, 20, 28-30, 36, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*3,* KUJC98117; *19,* KUJC98111; *20,* KUJC98115; *28,* KUJC98114; *29,* KUJC98113; *30,* KUJC98118; *36,* KUJC 98116).

Plate 4

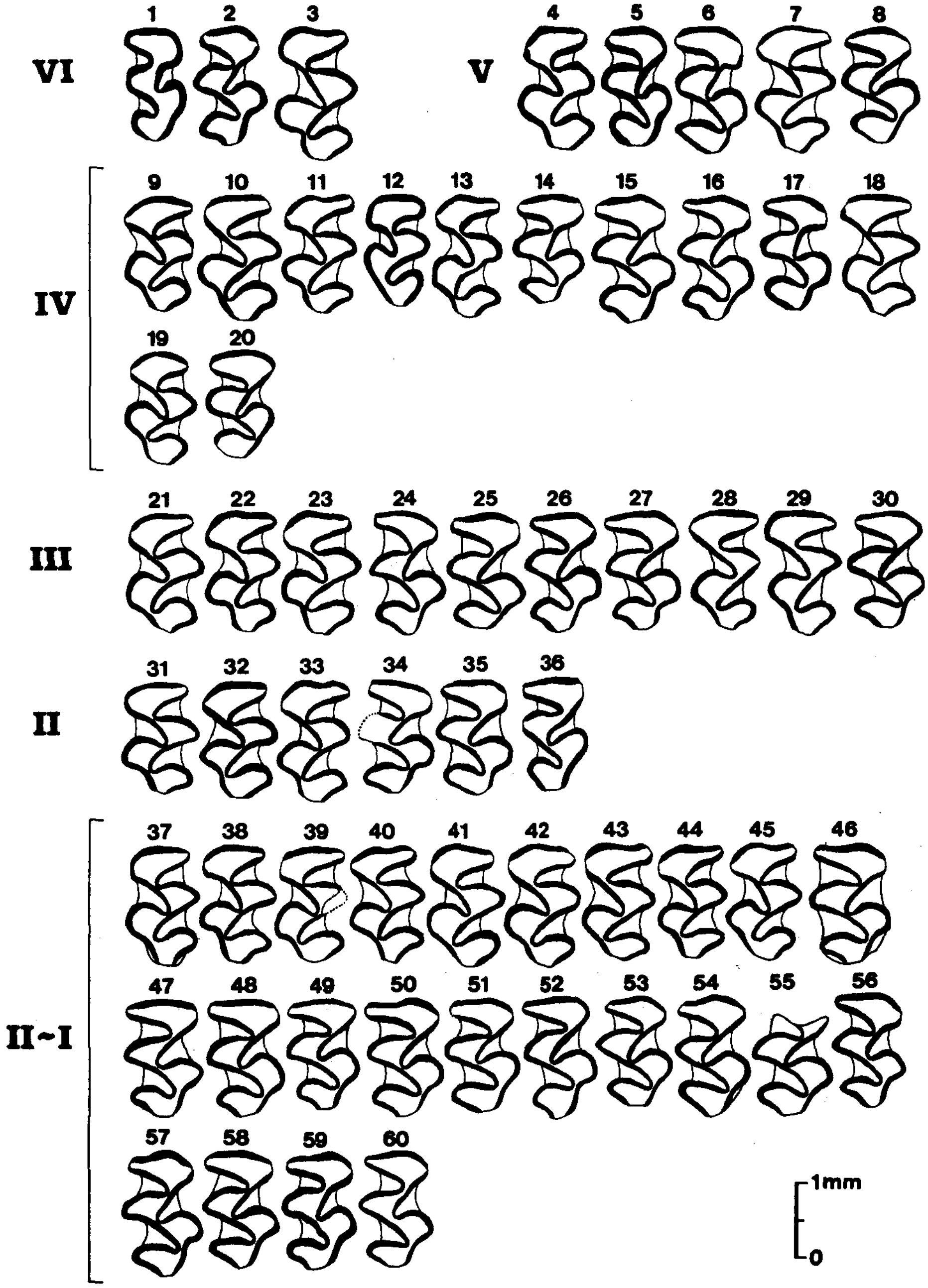
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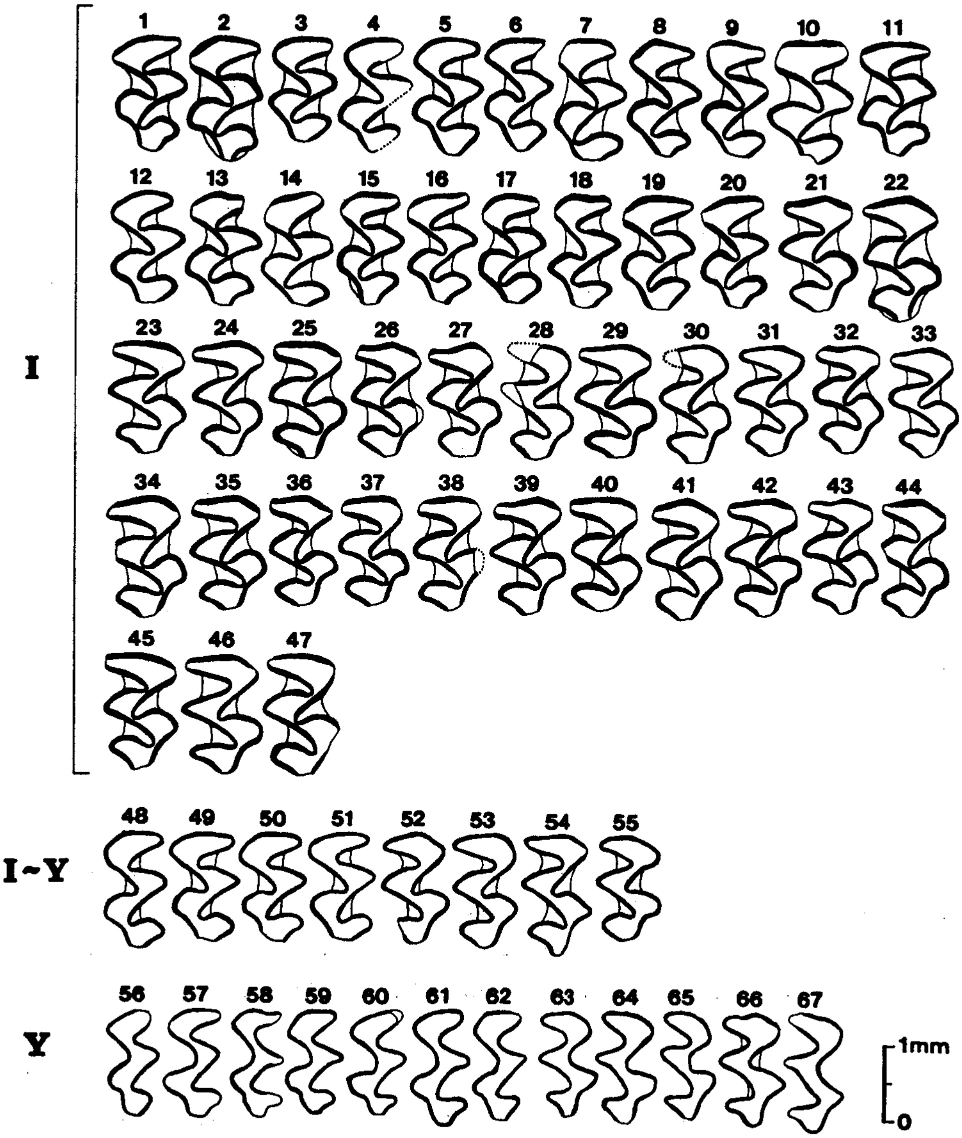
Plate 5

Clethrionomys japonicus, sp. nov.

Occlusal view of isolated M^2 from Locality 3 of Ube Kosan Quarry, showing the ontogenetic change in pattern from the age-classes I to Y.

1, KUJC96635 from Layer 1; *2*, KUJC96636 from Layer 1; *3*, KUJC96637 from Layer 1; *4*, KUJC96654 from Layer 2; *5*, KUJC96664 from Layer 3; *6*, KUJC96671 from Layer 4; *7*, KUJC 96742 from Layer 6; *8*, KUJC96715 from Layer 8; *9*, KUJC96702 from Layer 9; *10*, KUJC96703 from Layer 9; *11*, KUJC96695 from Layer 10; *12*, KUJC96696 from Layer 10; *13*, KUJC96738 from Layer 11; *14*, KUJC96735 from Layer 12; *15*, KUJC96731 from Layer 13; *16*, KUJC96732 from Layer 13; *17*, KUJC96722 from Layer 14; *18*, KUJC96723 from Layer 14; *19*, KUJC96690 from Layer 17; *20*, KUJC96681 from Layer 18; *21*, KUJC96630 from Layer 1; *22*, KUJC96644 from Layer 1; *23*, KUJC96645 from Layer 1; *24*, KUJC96646 from Layer 1; *25*, KUJC96648 from Layer 1; *26*, KUJC96649 from Layer 1; *27*, KUJC96652 from Layer 2; *28*, KUJC96657 from Layer 2; *29*, KUJC96667 from Layer 3; *30*, KUJC96668 from Layer 3; *31*, KUJC96677 from Layer 4; *32*, KUJC96678 from Layer 4; *33*, KUJC96679 from Layer 4; *34*, KUJC96747 from Layer 6; *35*, KUJC 96748 from Layer 6; *36*, KUJC96749 from Layer 6; *37*, KUJC96750 from Layer 6; *38*, KUJC 96717 from Layer 8; *39*, KUJC96707 from Layer 9; *40*, KUJC96708 from Layer 9; *41*, KUJC96709 from Layer 9; *42*, KUJC96710 from Layer 9; *43*, KUJC96736 from Layer 12; *44*, KUJC96727 from Layer 14; *45*, KUJC96691 from Layer 17; *46*, KUJC96692 from Layer 17; *47*, KUJC96683 from Layer 18; *48*, KUJC96655 from Layer 2; *49*, KUJC96659 from Layer 2; *50*, KUJC96672 from Layer 4; *51*, KUJC96673 from Layer 4; *52*, KUJC96676 from Layer 4; *53*, KUJC96680 from Layer 4; *54*, KUJC96688 from Layer 18; *55*, KUJC96689 from Layer 18; *56*, KUJC96638 from Layer 1; *57*, KUJC96650 from Layer 2; *58*, KUJC96743 from Layer 6; *59*, KUJC96716 from Layer 8; *60*, KUJC 96704 from Layer 9; *61*, KUJC96724 from Layer 14; *62*, KUJC96686 from Layer 18; *63*, KUJC 96653 from Layer 2; *64*, KUJC96711 from Layer 9; *65*, KUJC96701 from Layer 10; *66*, KUJC 96739 from Layer 11; *67*, KUJC96737 from Layer 12.

Plate 5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64
65
66
67
1mm
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Plate 6

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

Occlusal view of isolated M^3 showing the ontogenetic change in pattern from the age-classes VI to III-II.

1–3, 5–28, 33, 34, 36–47, 53–58, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1*, KUJC96497 from Layer 6; *2*, KUJC96398 from Layer 1; *3*, KUJC96454 from Layer 17; *5*, KUJC 96467 from Layer 9; *6*, KUJC96439 from Layer 3; *7*, KUJC96463 from Layer 10; *8*, KUJC96391 from Layer 1; *9*, KUJC96408 from Layer 2; *10*, KUJC96409 from Layer 2; *11*, KUJC96473 from Layer 8; *12*, KUJC96492 from Layer 13; *13*, KUJC96493 from Layer 13; *14*, KUJC96494 from Layer 13; *15*, KUJC96399 from Layer 1; *16*, KUJC96480 from Layer 8; *17*, KUJC96464 from Layer 10; *18*, KUJC96392 from Layer 1; *19*, KUJC96474 from Layer 8; *20*, KUJC96458 from Layer 10; *21*, KUJC 96496 from Layer 11; *22*, KUJC96389 from Layer 1; *23*, KUJC96400 from Layer 1; *24*, KUJC96417 from Layer 2; *25*, KUJC96429 from Layer 3; *26*, KUJC96430 from Layer 3; *27*, KUJC96481 from Layer 8; *28*, KUJC96471 from Layer 9; *33*, KUJC96450 from Layer 17; *34*, KUJC96445 from Layer 18; *36*, KUJC96393 from Layer 1; *37*, KUJC96394 from Layer 1; *38*, KUJC96425 from Layer 3; *39*, KUJC96475 from Layer 8; *40*, KUJC96476 from Layer 8; *41*, KUJC96401 from Layer 1; *42*, KUJC 96402 from Layer 1; *43*, KUJC96403 from Layer 1; *44*, KUJC96418 from Layer 2; *45*, KUJC96482 from Layer 8; *46*, KUJC96483 from Layer 8; *47*, KUJC96499=horizon unknown; *53*, KUJC96388 from Layer 1; *54*, KUJC96410 from Layer 2; *55*, KUJC96413 from Layer 2; *56*, KUJC96459 from Layer 10; *57*, KUJC96489 from Layer 14; *58*, KUJC96455 from Layer 17).

29, 35, 48, 59, *Clethrionomys japonicus* from Locality 1 of Ube Kosan Quarry (*29*, ASM 700044 from Layer 4b; *35*, ASM 700067 from Layer 2; *48*, ASM 700107 from Layer 1; *59*, ASM 700068 from Layer 2).

4, 30–32, 49–52, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*4*, KUJC98087; *30*, KUJC98088; *31*, KUJC98089; *32*, KUJC98100; *49*, KUJC98093; *50*, KUJC98094; *51*, KUJC 98095; *52*, KUJC98097).

Plate 6

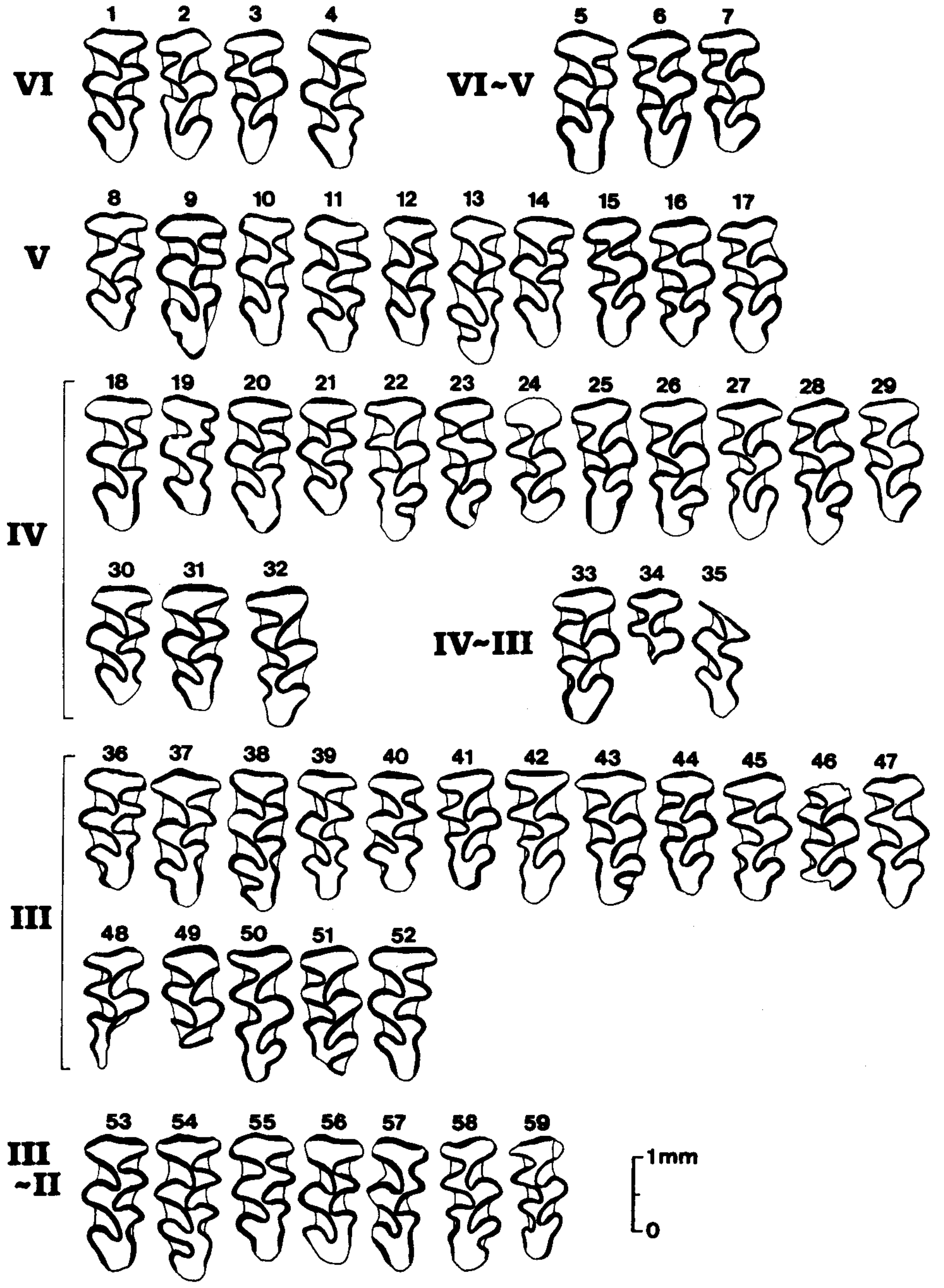
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Plate 7

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

Occlusal view of isolated M^3 showing the ontogenetic change in pattern from the age-classes II to Y.

1–30, 36–65, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1*, KUJC96395 from Layer 1; *2*, KUJC96396 from Layer 1; *3*, KUJC96397 from Layer 1; *4*, KUJC96414 from Layer 2; *5*, KUJC96415 from Layer 2; *6*, KUJC96426 from Layer 3; *7*, KUJC96427 from Layer 3; *8*, KUJC96435 from Layer 4; *9*, KUJC96436 from Layer 4; *10*, KUJC96452 from Layer 17; *11*, KUJC96460 from Layer 10; *12*, KUJC96477 from Layer 8; *13*, KUJC96404 from Layer 1; *14*, KUJC 96405 from Layer 1; *15*, KUJC96406 from Layer 1; *16*, KUJC96407 from Layer 1; *17*, KUJC96411 from Layer 2; *18*, KUJC96412 from Layer 2; *19*, KUJC96419 from Layer 2; *20*, KUJC96420 from Layer 2; *21*, KUJC96431 from Layer 3; *22*, KUJC96432 from Layer 3; *23*, KUJC96440 from Layer 3; *24*, KUJC96484 from Layer 8; *25*, KUJC96472 from Layer 9; *26*, KUJC96465 from Layer 10; *27*, KUJC96466 from Layer 10; *28*, KUJC96451 from Layer 17; *29*, KUJC96456 from Layer 17; *30*, KUJC96448 from Layer 18; *36*, KUJC96414 from Layer 2; *37*, KUJC96428 from Layer 3; *38*, KUJC96478 from Layer 8; *39*, KUJC96479 from Layer 8; *40*, KUJC96495 from Layer 13; *41*, KUJC96468 from Layer 9; *42*, KUJC96469 from Layer 9; *43*, KUJC96461 from Layer 10; *44*, KUJC 96462 from Layer 10; *45*, KUJC96421 from Layer 2; *46*, KUJC96422 from Layer 2; *47*, KUJC96433 from Layer 3; *48*, KUJC96434 from Layer 3; *49*, KUJC96441 from Layer 4; *50*, KUJC96498 from Layer 6; *51*, KUJC96485 from Layer 8; *52*, KUJC96486 from Layer 8; *53*, KUJC96487 from Layer 8; *54*, KUJC96491 from Layer 14; *55*, KUJC96490 from Layer 14; *56*, KUJC96453 from Layer 17; *57*, KUJC96457 from Layer 17; *58*, KUJC96423 from Layer 2; *59*, KUJC96437 from Layer 4; *60*, KUJC96438 from Layer 4; *61*, KUJC96470 from Layer 9; *62*, KUJC96424 from Layer 2; *63*, KUJC 96442 from Layer 3; *64*, KUJC96488 from Layer 8; *65*, KUJC96449 from Layer 18).

31, *Clethrionomys japonicus* from Ikumo Quarry (ASM 700006).

32–35, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*32*, KUJC98091; *33*, KUJC 98092; *34*, KUJC98096; *35*, KUJC98098).

Plate 7

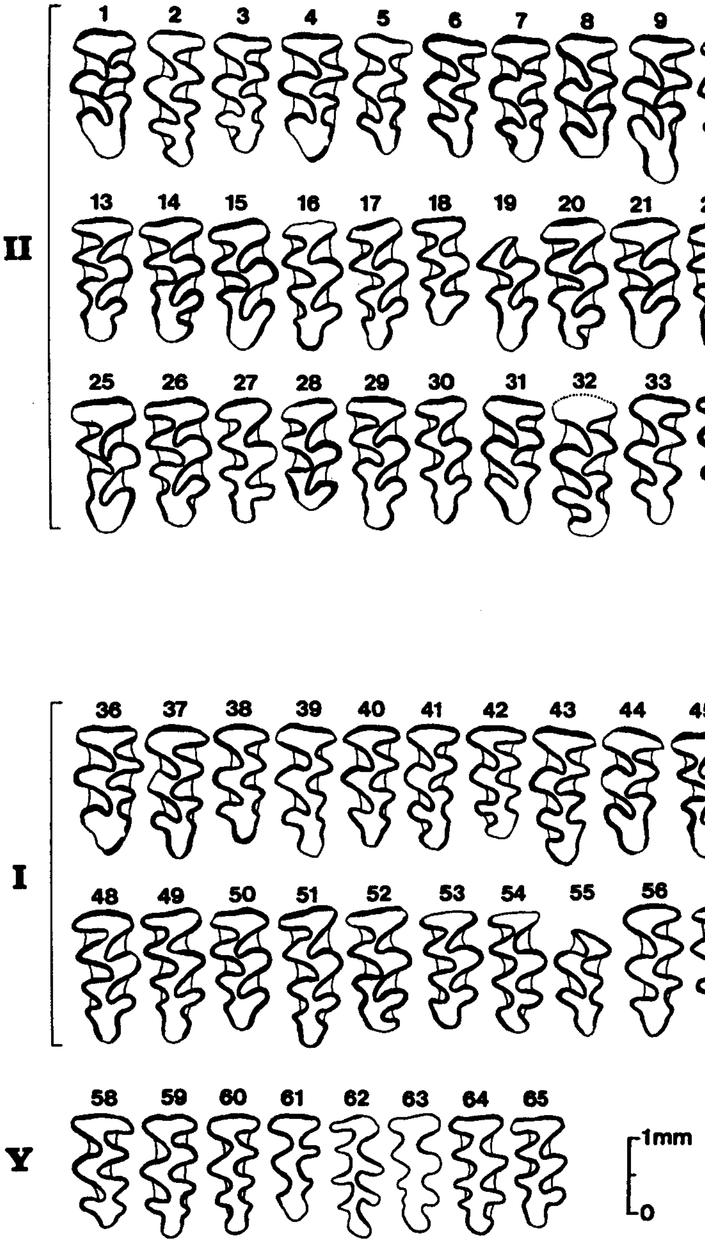
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Plate 8

Clethrionomys japonicus, sp. nov.

Occlusal view of lower molar rows from Locality 3 of Ube Kosan Quarry.

1–2, left M_1 to M_3 (*1*, KUJC96326 from Layer 4; *2*, KUJC96324 from Layer 4); **3–6,** right M_1 to M_3 (*3*, KUJC96328 from Layer 4; *4*, KUJC96330 from Layer 4; *5*, KUJC96342 from Layer 17; *6*, KUJC96501=horizon unknown); **7–12,** left M_1 and M_2 (*7*, KUJC96280 from Layer 1; *8*, KUJC 96299 from Layer 2; *9*, KUJC96311 from Layer 3; *10*, KUJC96312 from Layer 3; *11*, KUJC96325 from Layer 4; *12*, KUJC96354 from Layer 8); **13–20,** right M_1 and M_2 (*13*, KUJC96275 from Layer 1; *14*, KUJC96296 from Layer 1; *15*, KUJC96282 from Layer 1; *16*, KUJC96295 from Layer 1; *17*, KUJC96300 from Layer 2; *18*, KUJC96307 from Layer 2; *19*, KUJC96308 from Layer 2; *20*, KUJC96313 from Layer 3); **21,** left M_2 and M_3 (KUJC96302 from Layer 2); **22,** right M_2 and M_3 (KUJC96502=horizon unknown); **23–26,** right M_1 and M_2 (*23*, KUJC96314 from Layer 3; *24*, KUJC96329 from Layer 4; *25*, KUJC96331 from Layer 4; *26*, KUJC96339 from Layer 17).

Plate 8

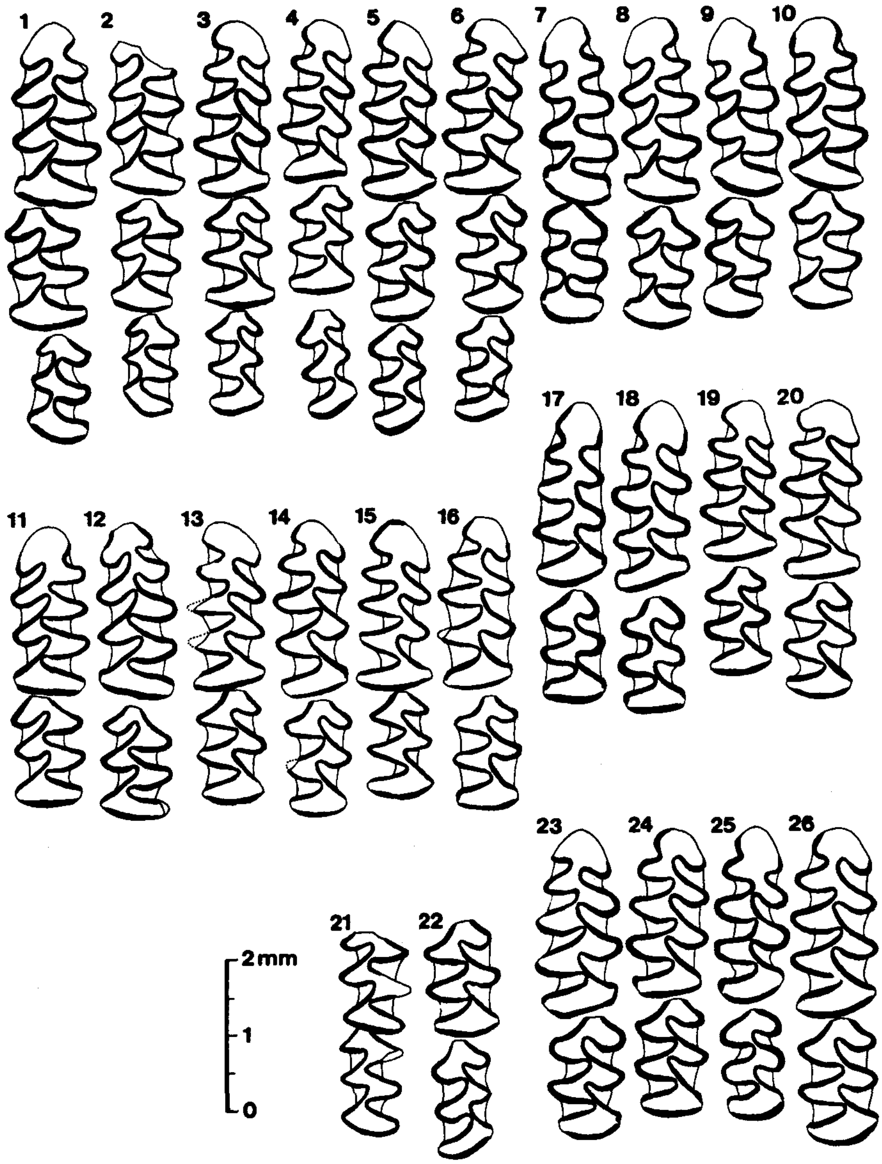


Plate 9

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

Occlusal view of M_1 showing the ontogenetic change in pattern from the age-classes VI to IV-III.

1–3, 16, 19, 21–27, 32, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1*, KUJC96316 from Layer 3; *2*, KUJC96380 from Layer 11; *3*, KUJC96364 from Layer 5; *16*, KUJC96381 from Layer 6; *19*, KUJC96301 from Layer 2; *21*, KUJC96283 from Layer 1; *22*, KUJC96379 from Layer 12; *23*, KUJC96291 from Layer 1; *24*, KUJC96385 from Layer 6; *25*, KUJC96350 from Layer 9; *26*, KUJC96345 from Layer 10; *27*, KUJC96291 from Layer 1; *32*, KUJC96276 from Layer 1).

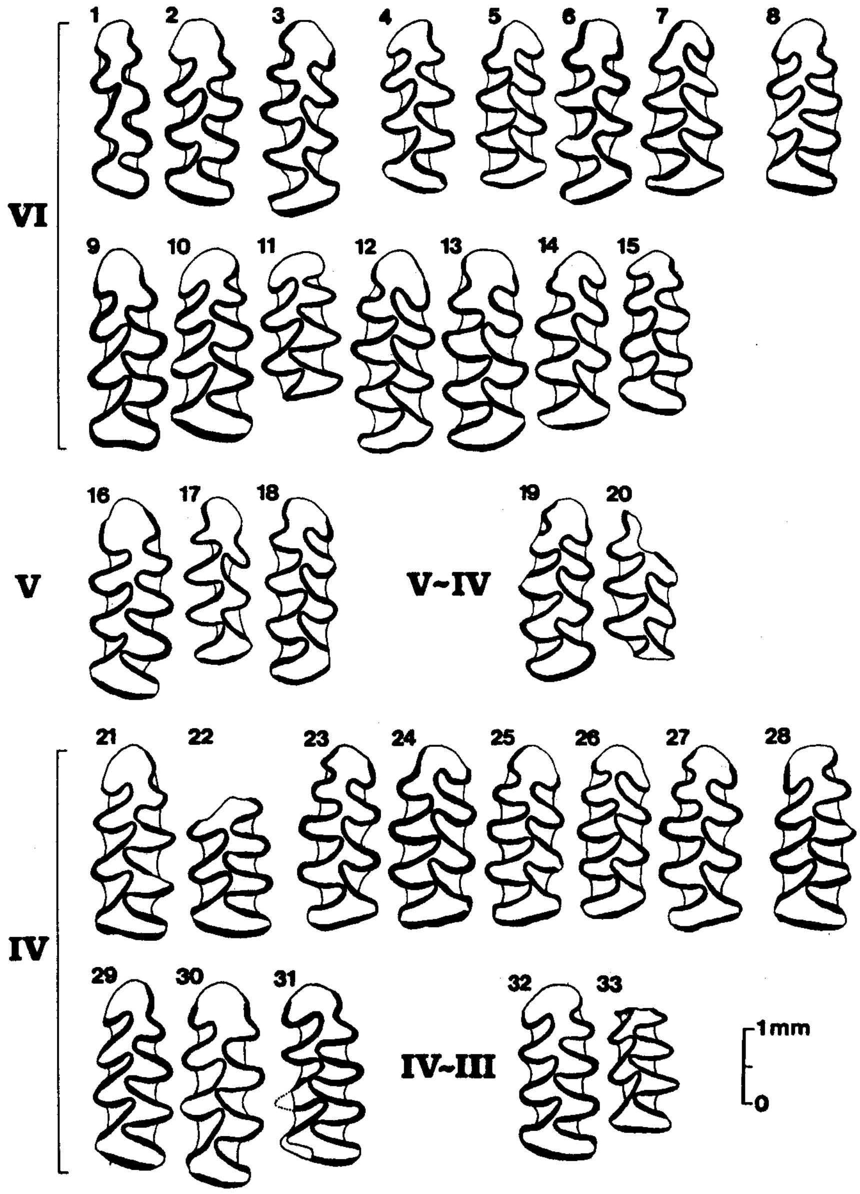
4–7, 17, 20, 28, 33, *Clethrionomys japonicus* from Layer 2 of Locality 1 of Ube Kosan Quarry (*4*, ASM 700078; *5*, ASM 700081; *6*, ASM 700084; *7*, ASM 700085; *17*, ASM 700086; *20*, ASM 700082; *28*, ASM 700076; *33*, ASM 700080).

8, *Clethrionomys japonicus* from Ikumo Quarry (ASM 700003).

9–15, 18, 29, 30, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*9*, KUJC98067; *10*, KUJC98068; *11*, KUJC98081; *12*, KUJC98077; *13*, KUJC98078; *14*, KUJC98079; *15*, KUJC 98080; *18*, KUJC98085; *29*, KUJC98069; *30*, KUJC98072).

31, *Clethrionomys-Phaulomys* transitional form from Kumaishi-do Cave (YKS 00021).

Plate 9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V
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V~IV
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30
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IV~III
32
33
1mm
0

Plate 10

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

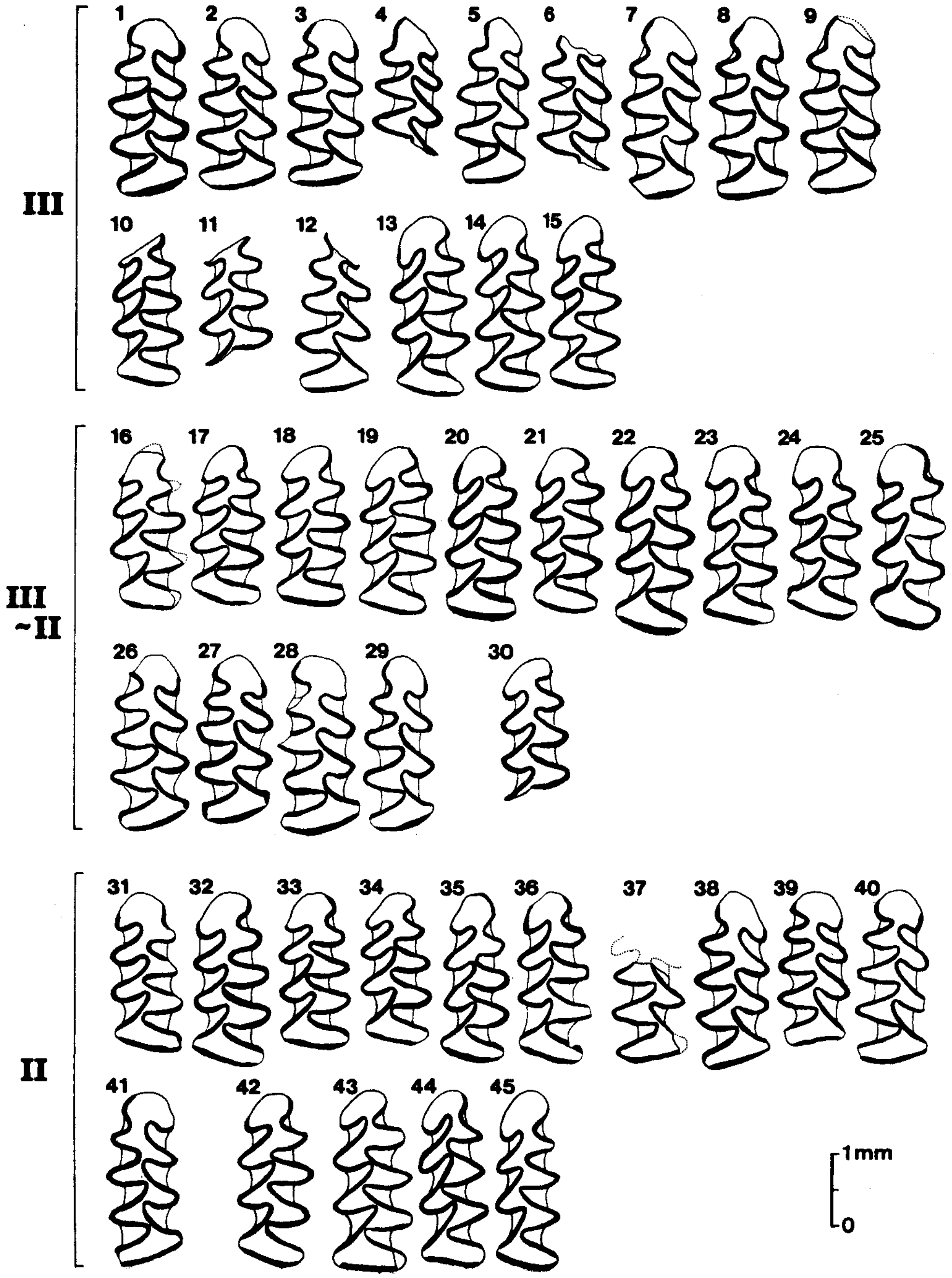
Occlusal view of isolated M_1 showing the ontogenetic change in pattern from the age-classes III to II.

1–9, 16–29, 31–41, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1*, KUJC96386 from Layer 6; *2*, KUJC96357 from Layer 8; *3*, KUJC96358 from Layer 8; *4*, KUJC96359 from Layer 8; *5*, KUJC96365 from Layer 8; *6*, KUJC96366 from Layer 8; *7*, KUJC96351 from Layer 9; *8*, KUJC96352 from Layer 9; *9*, KUJC96346 from Layer 10; *16*, KUJC96284 from Layer 1; *17*, KUJC 96285 from Layer 1; *18*, KUJC96286 from Layer 1; *19*, KUJC96287 from Layer 1; *20*, KUJC96305 from Layer 2; *21*, KUJC96382 from Layer 6; *22*, KUJC96349 from Layer 9; *23*, KUJC96372 from Layer 13; *24*, KUJC96373 from Layer 13; *25*, KUJC96337 from Layer 18; *26*, KUJC96278 from Layer 1; *27*, KUJC96292 from Layer 1; *28*, KUJC96333 from Layer 4; *29*, KUJC96338 from Layer 18; *31*, KUJC96304 from Layer 2; *32*, KUJC96317 from Layer 3; *33*, KUJC96318 from Layer 3; *34*, KUJC96355 from Layer 8; *35*, KUJC96374 from Layer 13; *36*, KUJC96343 from Layer 17; *37*, KUJC96387 from Layer 6; *38*, KUJC96360 from Layer 8; *39*, KUJC96361 from Layer 8; *40*, KUJC 96347 from Layer 10; 41, KUJC96377 from Layer 13).

10–12, 30, 42, *Clethrionomys japonicus* from Locality 1 of Ube Kosan Quarry (*10*, ASM 700077 from Layer 2; *11*, ASM 700079 from Layer 2; *12*, ASM 700049 from Layer 3b; *30*, ASM 700108 from Layer 1; *42*, ASM 700075 from Layer 2).

13–15, 43–45, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*13*, KUJC98071; *14*, KUJC98082; *15*, KUJC98083; *43*, KUJC98074; *44*, KUJC98075; *45*, KUJC98084).

Plate 10


III
1 2 3 4 5 6 7 8 9
10 11 12 13 14 15
III ~II
16 17 18 19 20 21 22 23 24 25
26 27 28 29 30
II
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41 42 43 44 45
1mm
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Plate 11

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

Occlusal view of isolated M_1 showing the ontogenetic change in pattern from the age-classes II-I to Y.

1–5, 10–36, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1*, KUJC96383 from Layer 6; *2*, KUJC96371 from Layer 13; *3*, KUJC96340 from Layer 17; *4*, KUJC96334 from Layer 4; *5*, KUJC96370 from Layer 14; *10*, KUJC96277 from Layer 1; *11*, KUJC96288 from Layer 1; *12*, KUJC96289 from Layer 1; *13*, KUJC96309 from Layer 2; *14*, KUJC96319 from Layer 3; *15*, KUJC96320 from Layer 3; *16*, KUJC96332 from Layer 4; *17*, KUJC96384 from Layer 6; *18*, KUJC 96356 from Layer 8; *19*, KUJC96375 from Layer 13; *20*, KUJC96376 from Layer 13; *21*, KUJC 96368 from Layer 14; *22*, KUJC96344 from Layer 10; *23*, KUJC96279 from Layer 1; *24*, KUJC 96293 from Layer 1; *25*, KUJC96294 from Layer 1; *26*, KUJC96297 from Layer 1; *27*, KUJC96298 from Layer 1; *28*, KUJC96306 from Layer 2; *29*, KUJC96322 from Layer 3; *30*, KUJC96323 from Layer 3; *31*, KUJC96335 from Layer 4; *32*, KUJC96362 from Layer 8; *33*, KUJC96363 from Layer 8; *34*, KUJC96353 from Layer 9; *35*, KUJC96348 from Layer 10; *36*, KUJC96378 from Layer 13).

6, 37, 38, *Clethrionomys japonicus* from Layer 2 of Locality 1 of Ube Kosan Quarry (*6*, ASM 700083; *37*, ASM 700074; *38*, ASM 700087).

7–9, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*7*, KUJC98070; *8*, KUJC 98073; *9*, KUJC98086).

Plate 11

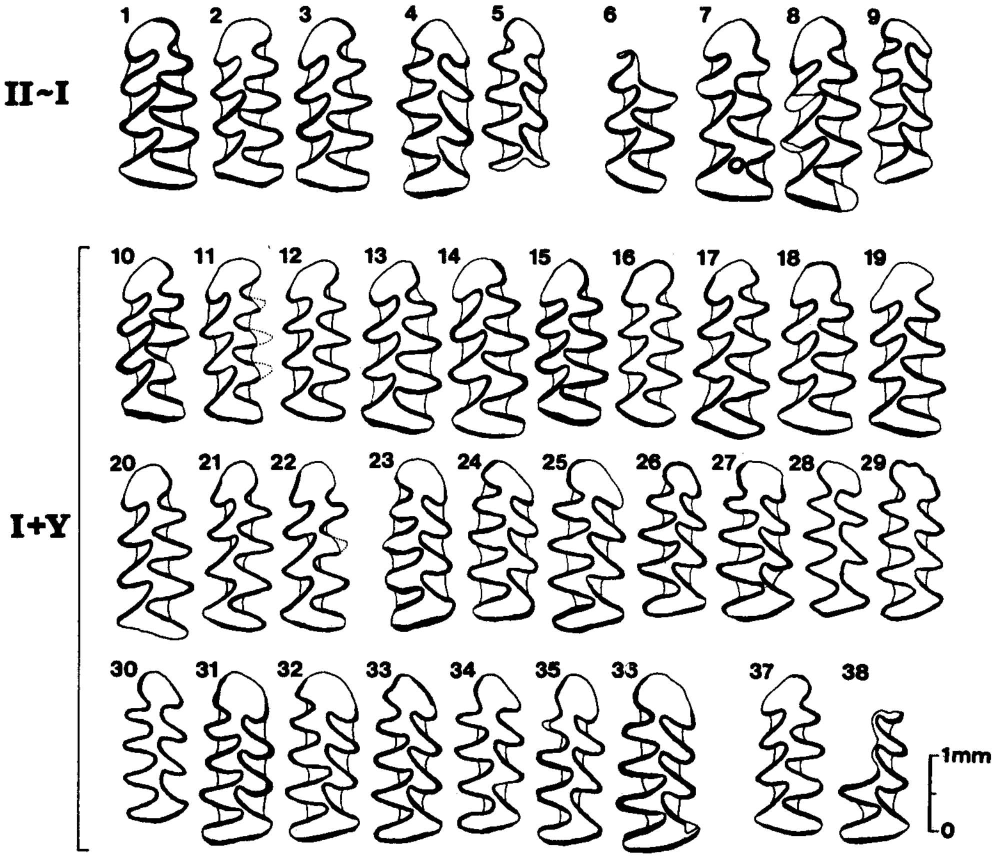
II~I
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Plate 12

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

Occlusal view of isolated M_2 showing the ontogenetic change in pattern from the age-classes VI to II-I.

1–6, 10–20, 25–50, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1*, KUJC96771 from Layer 2; *2*, KUJC96858 from Layer 11; *3*, KUJC96777 from Layer 2; *4*, KUJC96776 from Layer 2; *5*, KUJC96839 from Layer 5; *6*, KUJC96806 from Layer 17; *10*, KUJC96780 from Layer 2; *11*, KUJC96821 from Layer 9; *12*, KUJC96822 from Layer 9; *13*, KUJC96844 from Layer 14; *14*, KUJC 96856 from Layer 12; *15*, KUJC96859 from Layer 6; *16*, KUJC96768 from Layer 1; *17*, KUJC 96785 from Layer 3; *18*, KUJC96794 from Layer 4; *19*, KUJC96861 from Layer 6; *20*, KUJC96832 from Layer 8; *25*, KUJC96753 from Layer 1; *26*, KUJC96759 from Layer 1; *27*, KUJC96772 from Layer 2; *28*, KUJC96774 from Layer 2; *29*, KUJC96788 from Layer 4; *30*, KUJC96838 from Layer 8; *31*, KUJC96828 from Layer 8; *32*, KUJC96756 from Layer 1; *33*, KUJC96786 from Layer 3; *34*, KUJC96812 from Layer 10; *35*, KUJC96823 from Layer 9; *36*, KUJC96758 from Layer 1; *37*, KUJC96760 from Layer 1; *38*, KUJC96789 from Layer 4; *39*, KUJC96860 from Layer 6; *40*, KUJC 96817 from Layer 9; *41*, KUJC96818 from Layer 9; *42*, KUJC96807 from Layer 10; *43*, KUJC 96846 from Layer 13; *44*, KUJC96847 from Layer 13; *45*, KUJC96840 from Layer 14; *46*, KUJC 96799 from Layer 18; *47*, KUJC96757 from Layer 1; *48*, KUJC96769 from Layer 1; *49*, KUJC 96862 from Layer 6; *50*, KUJC96814 from Layer 10.

9, *Clethrionomys japonicus* from Ikumo Quarry (ASM 700004).

7, 21–24, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*7*, KUJC98121; *21*, KUJC 98122; *22*, KUJC98123; *23*, KUJC98124; *24*, KUJC98125).

8, *Clethrionomys-Phaulomys* transitional form from F_4 of Kumaishi-do Cave (YKS 00823).

Plate 12

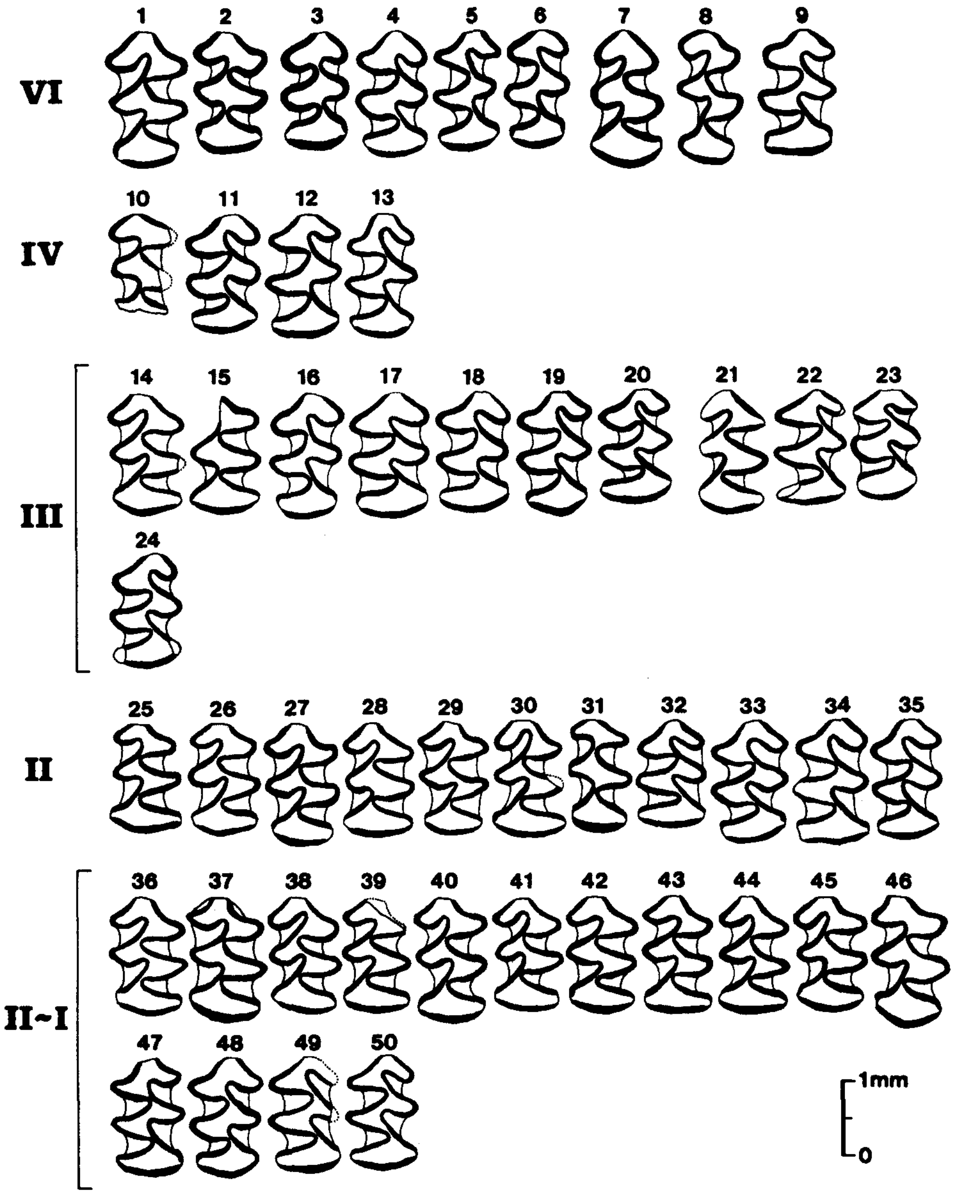
VI
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Plate 13

Clethrionomys japonicus, sp. nov.

Occlusal view of isolated M_2 showing the ontogenetic change in pattern from the age-classes I to Y.

1–37, 40–62, M_2 from Locality 3 of Ube Kosan Quarry (*1*, KUJC96761 from Layer 1; *2*, KUJC 96762 from Layer 1; *3*, KUJC96763 from Layer 1; *4*, KUJC96764 from Layer 1; *5*, KUJC96765 from Layer 1; *6*, KUJC96775 from Layer 2; *7*, KUJC96782 from Layer 3; *8*, KUJC96783 from Layer 3; *9*, KUJC96784 from Layer 3; *10*, KUJC96829 from Layer 8; *11*, KUJC96819 from Layer 9; *12*, KUJC96808 from Layer 10; *13*, KUJC96809 from Layer 10; *14*, KUJC96848 from Layer 13; *15*, KUJC96849 from Layer 13; *16*, KUJC96850 from Layer 13; *17*, KUJC96841 from Layer 14; *18*, KUJC96770 from Layer 1; *19*, KUJC96778 from Layer 2; *20*, KUJC96787 from Layer 3; *21*, KUJC96795 from Layer 4; *22*, KUJC96796 from Layer 4; *23*, KUJC96863 from Layer 6; *24*, KUJC96864 from Layer 6; *25*, KUJC96833 from Layer 8; *26*, KUJC96834 from Layer 8; *27*, KUJC 96835 from Layer 8; *28*, KUJC96836 from Layer 8; *29*, KUJC96837 from Layer 8; *30*, KUJC96824 from Layer 9; *31*, KUJC96825 from Layer 9; *32*, KUJC96815 from Layer 10; *33*, KUJC96852 from Layer 13; *34*, KUJC96853 from Layer 13; *35*, KUJC96845 from Layer 14; *36*, KUJC96804 from Layer 18; *37*, KUJC96827 from Layer 9; *40*, KUJC96754 from Layer 1; *41*, KUJC96755 from Layer 1; *42*, KUJC96766 from Layer 1; *43*, KUJC96790 from Layer 4; *44*, KUJC96791 from Layer 4; *45*, KUJC96792 from Layer 4; *46*, KUJC96830 from Layer 8; *47*, KUJC96820 from Layer 9; *48*, KUJC 96810 from Layer 10; *49*, KUJC96811 from Layer 10; *50*, KUJC96800 from Layer 18; *51*, KUJC 96779 from Layer 2; *52*, KUJC96797 from Layer 4; *53*, KUJC96798 from Layer 4; *54*, KUJC 96816 from Layer 10; *55*, KUJC96802 from Layer 18; *56*, KUJC96767 from Layer 1; *57*, KUJC 96773 from Layer 2; *58*, KUJC96781 from Layer 2; *59*, KUJC96793 from Layer 4; *60*, KUJC96851 from Layer 13; *61*, KUJC96842 from Layer 14; *62*, KUJC96854 from Layer 13).

38, 39, M_2 from Layer 2 of Locality 1 of Ube Kosan Quarry (*38*, ASM 700089; *39*, ASM 700090).

Plate 13

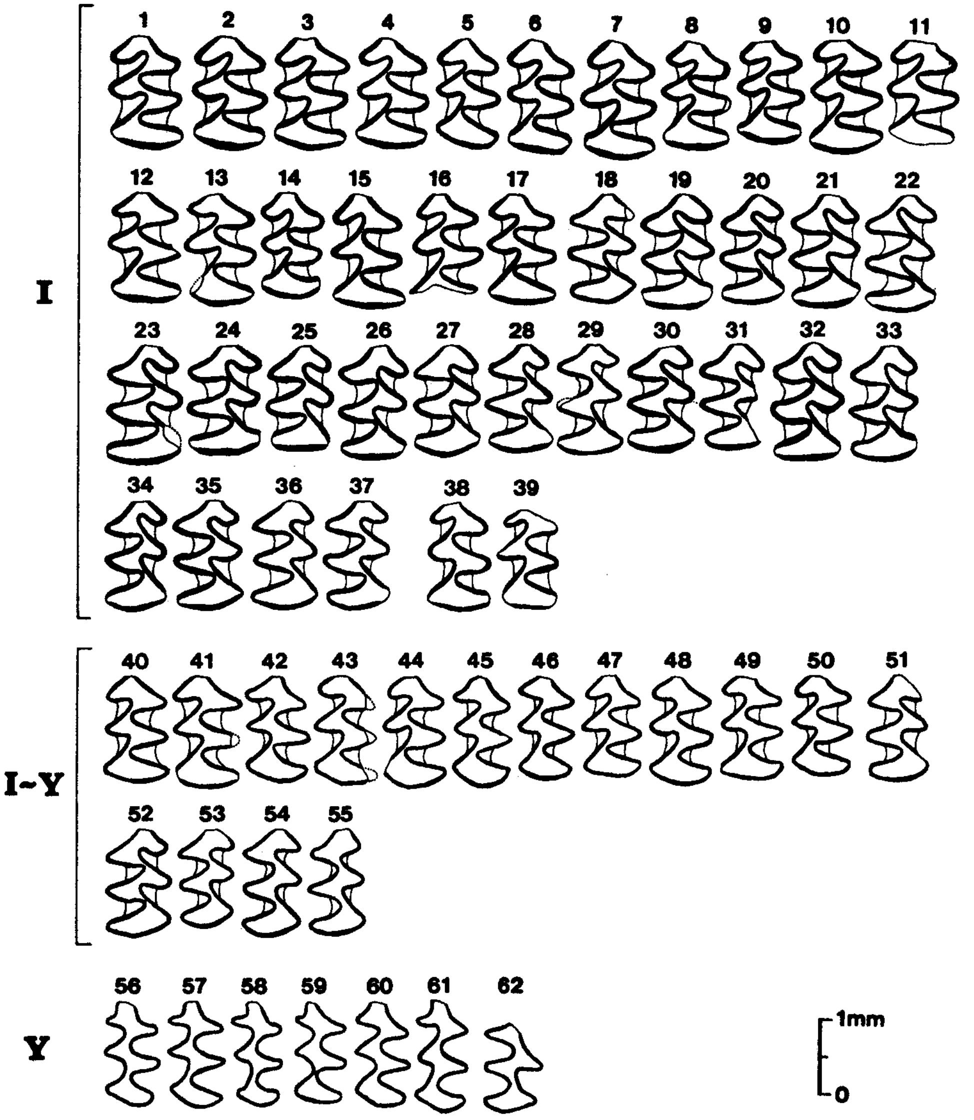
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Plate 14

Clethrionomys japonicus, sp. nov. and *Clethrionomys-Phaulomys* transitional form

Occlusal view of isolated M_3 showing the ontogenetic change in pattern from the age-classes VI to II.

1–9, 12–19, 23–31, 38–57, *Clethrionomys japonicus* from Locality 3 of Ube Kosan Quarry (*1*, KUJC 96869 from Layer 1; *2*, KUJC96910 from Layer 3; *3*, KUJC96911 from Layer 3; *4*, KUJC96980 from Layer 11; *5*, KUJC96967 from Layer 5; *6*, KUJC96891 from Layer 2; *7*, KUJC96956 from Layer 8; *8*, KUJC96972 from Layer 13; *9*, KUJC96907 from Layer 2; *12*, KUJC96870 from Layer 1; *13*, KUJC96871 from Layer 1; *14*, KUJC96912 from Layer 3; *15*, KUJC96878 from Layer 1; *16*, KUJC96879 from Layer 1; *17*, KUJC96887 from Layer 1; *18*, KUJC96903 from Layer 2; *19*, KUJC96979 from Layer 12; *23*, KUJC96889 from Layer 2; *24*, KUJC96937 from Layer 18; *25*, KUJC96981 from Layer 6; *26*, KUJC96957 from Layer 8; *27*, KUJC96978 from Layer 12; *28*, KUJC96925 from Layer 4; *29*, KUJC96985 from Layer 6; *30*, KUJC96950 from Layer 9; *31*, KUJC 96951 from Layer 9; *38*, KUJC96865 from Layer 1; *39*, KUJC96872 from Layer 1; *40*, KUJC96873 from Layer 1; *41*, KUJC96874 from Layer 1; *42*, KUJC96892 from Layer 2; *43*, KUJC96913 from Layer 3; *44*, KUJC96982 from Layer 6; *45*, KUJC96973 from Layer 13; *46*, KUJC96974 from Layer 13; *47*, KUJC96975 from Layer 13; *48*, KUJC96968 from Layer 14; *49*, KUJC96933 from Layer 18; *50*, KUJC96919 from Layer 3; *51*, KUJC96926 from Layer 4; *52*, KUJC96927 from Layer 4; *53*, KUJC96928 from Layer 4; *54*, KUJC96961 from Layer 8; *55*, KUJC96962 from Layer 8; *56*, KUJC 96953 from Layer 9; *57*, KUJC96943 from Layer 10).

10, *Clethrionomys japonicus* from Ikumo Quarry (ASM 700005).

20, 32–34, *Clethrionomys japonicus* from Layer 2 of Locality 1 of Ube Kosan Quarry (*20*, ASM 700097; *32*, ASM 700096; *33*, ASM 700095; *34*, ASM 700100).

11, 21, 22, 35–37, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave (*11*, KUJC98128; *21*, KUJC98129; *22*, KUJC98134; *35*, KUJC98126; *36*, KUJC98130; *37*, KUJC98133).

Plate 14

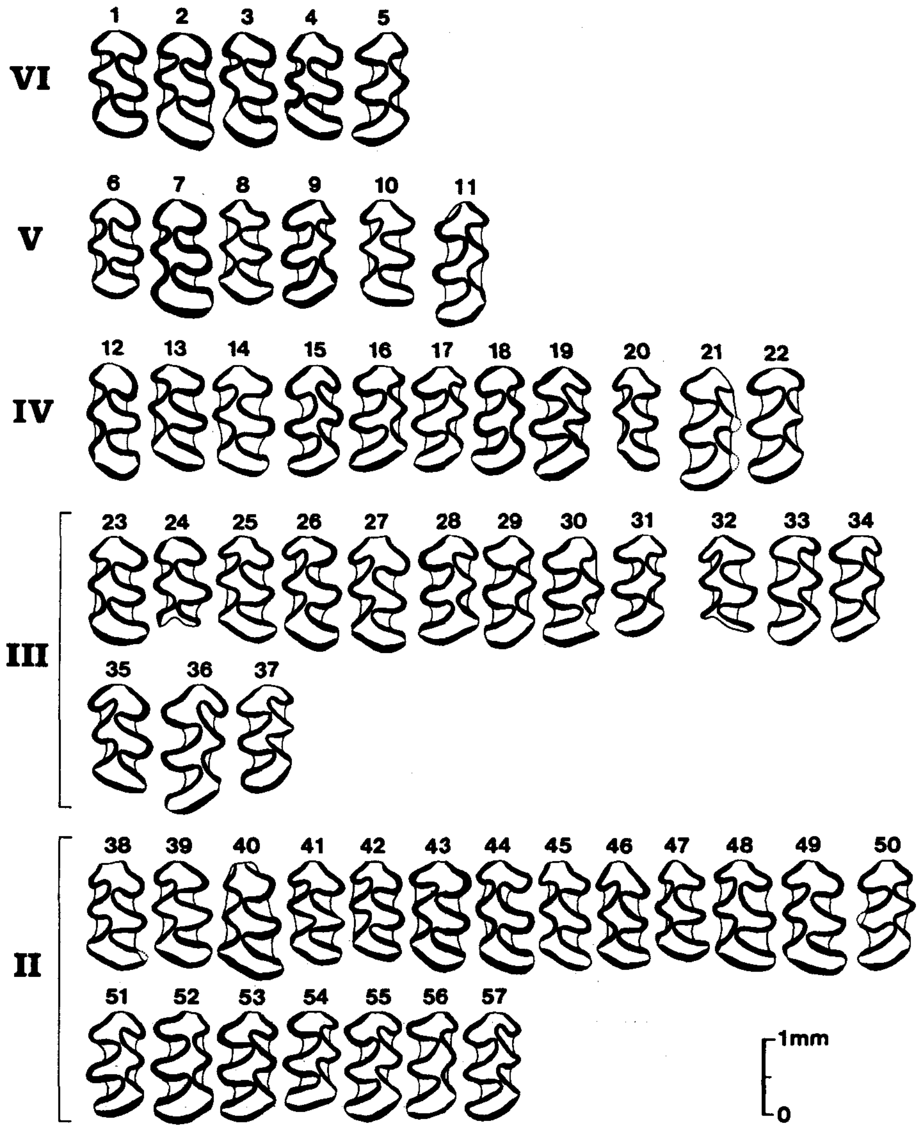
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Plate 15

Clethrionomys japonicus, sp. nov.

Occlusal view of isolated M_3 showing the ontogenetic change in pattern from the age-classes I to Y.

1–52, 56–78, M_3 from Locality 3 of Ube Kosan Quarry (*1*, KUJC96866 from Layer 1; *2*, KUJC 96875 from Layer 1; *3*, KUJC96876 from Layer 1; *4*, KUJC96886 from Layer 1; *5*, KUJC96893 from Layer 2; *6*, KUJC96894 from Layer 2; *7*, KUJC96895 from Layer 2; *8*, KUJC96896 from Layer 2; *9*, KUJC96897 from Layer 2; *10*, KUJC96914 from Layer 3; *11*, KUJC96915 from Layer 3; *12*, KUJC96916 from Layer 3; *13*, KUJC96923 from Layer 4; *14*, KUJC96983 from Layer 6; *15*, KUJC 96958 from Layer 8; *16*, KUJC96959 from Layer 8; *17*, KUJC96948 from Layer 9; *18*, KUJC96949 from Layer 9; *19*, KUJC96941 from Layer 10; *20*, KUJC96976 from Layer 13; *21*, KUJC96969 from Layer 14; *22*, KUJC96986=horizon unknown; *23*, KUJC96868 from Layer 1; *24*, KUJC96880 from Layer 1; *25*, KUJC96881 from Layer 1; *26*, KUJC96882 from Layer 1; *27*, KUJC96884 from Layer 1; *28*, KUJC96888 from Layer 1; *29*, KUJC96890 from Layer 2; *30*, KUJC96908 from Layer 2; *31*, KUJC96920 from Layer 3; *32*, KUJC96921 from Layer 3; *33*, KUJC96929 from Layer 4; *34*, KUJC96930 from Layer 4; *35*, KUJC96931 from Layer 4; *36*, KUJC96963 from Layer 8; *37*, KUJC 96964 from Layer 8; *38*, KUJC96965 from Layer 8; *39*, KUJC96966 from Layer 8; *40*, KUJC96954 from Layer 9; *41*, KUJC96955 from Layer 9; *42*, KUJC96944 from Layer 10; *43*, KUJC96945 from Layer 10; *44*, KUJC96746 from Layer 10; *45*, KUJC96747 from Layer 10; *46*, KUJC96970 from Layer 14; *47*, KUJC96971 from Layer 14; *48*, KUJC96939 from Layer 17; *49*, KUJC96940 from Layer 17; *50*, KUJC96935 from Layer 18; *51*, KUJC96936 from Layer 18; *52*, KUJC96988=horizon unknown; *56*, KUJC96867 from Layer 1; *57*, KUJC96877 from Layer 1; *58*, KUJC96898 from Layer 2; *59*, KUJC96900 from Layer 2; *60*, KUJC96924 from Layer 4; *61*, KUJC96984 from Layer 6; *62*, KUJC96942 from Layer 10; *63*, KUJC96934 from Layer 18; *64*, KUJC96938 from Layer 18; *65*, KUJC96977 from Layer 13; *66*, KUJC96885 from Layer 1; *67*, KUJC96883 from Layer 1; *68*, KUJC96901 from Layer 2; *69*, KUJC96902 from Layer 2; *70*, KUJC96905 from Layer 2; *71*, KUJC96906 from Layer 2; *72*, KUJC96917 from Layer 3; *73*, KUJC96960 from Layer 8; *74*, KUJC96987=horizon unknown; *75*, KUJC96904 from Layer 2; *76*, KUJC96909 from Layer 2; *77*, KUJC96922 from Layer 3; *78*, KUJC96932 from Layer 4.

53, M_3 from Ikumo Quarry (ASM 700008)

54, 55, M_3 from Layer 2 of Locality 1 of Ube Kosan Quarry (*54*, ASM 700098; *55*, ASM 700099).

Plate 15

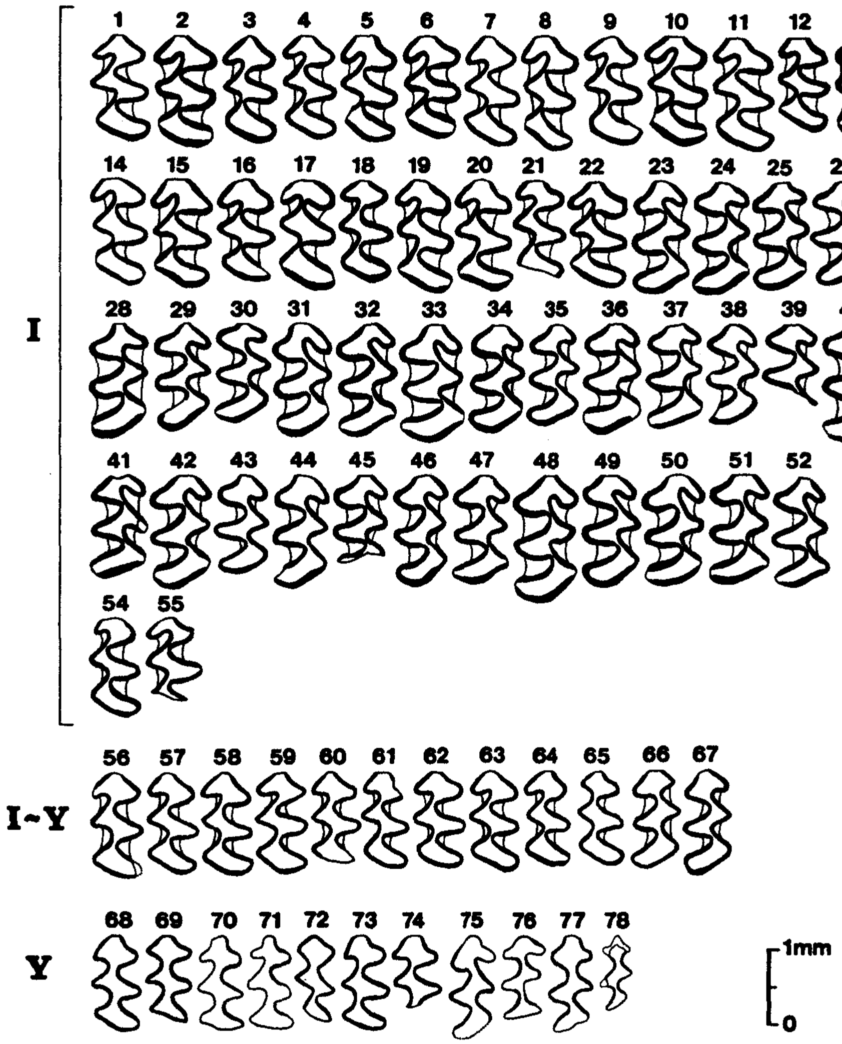
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Plate 16

Clethrionomys-Phaulomys **transitional form**

Occlusal view of isolated M_1 without sign of root-formation.

1–28, left M_1 from Sugi-ana Cave (KUJC99178 to 99205 respectively); **29–62**, right M_1 from the same cave (KUJC99206 to 99239 respectively).

63–70, left M_1 from F_1, F_2 and F_4 of Kumaishi-do Cave (*63*, YKS 00067; *64*, YKS 00094; *65*, YKS 00098; *66*, YKS 00104; *67*, YKS 00029; *68*, YKS 00037; *69*, YKS 00078; *70*, YKS 00101).

Plate 16

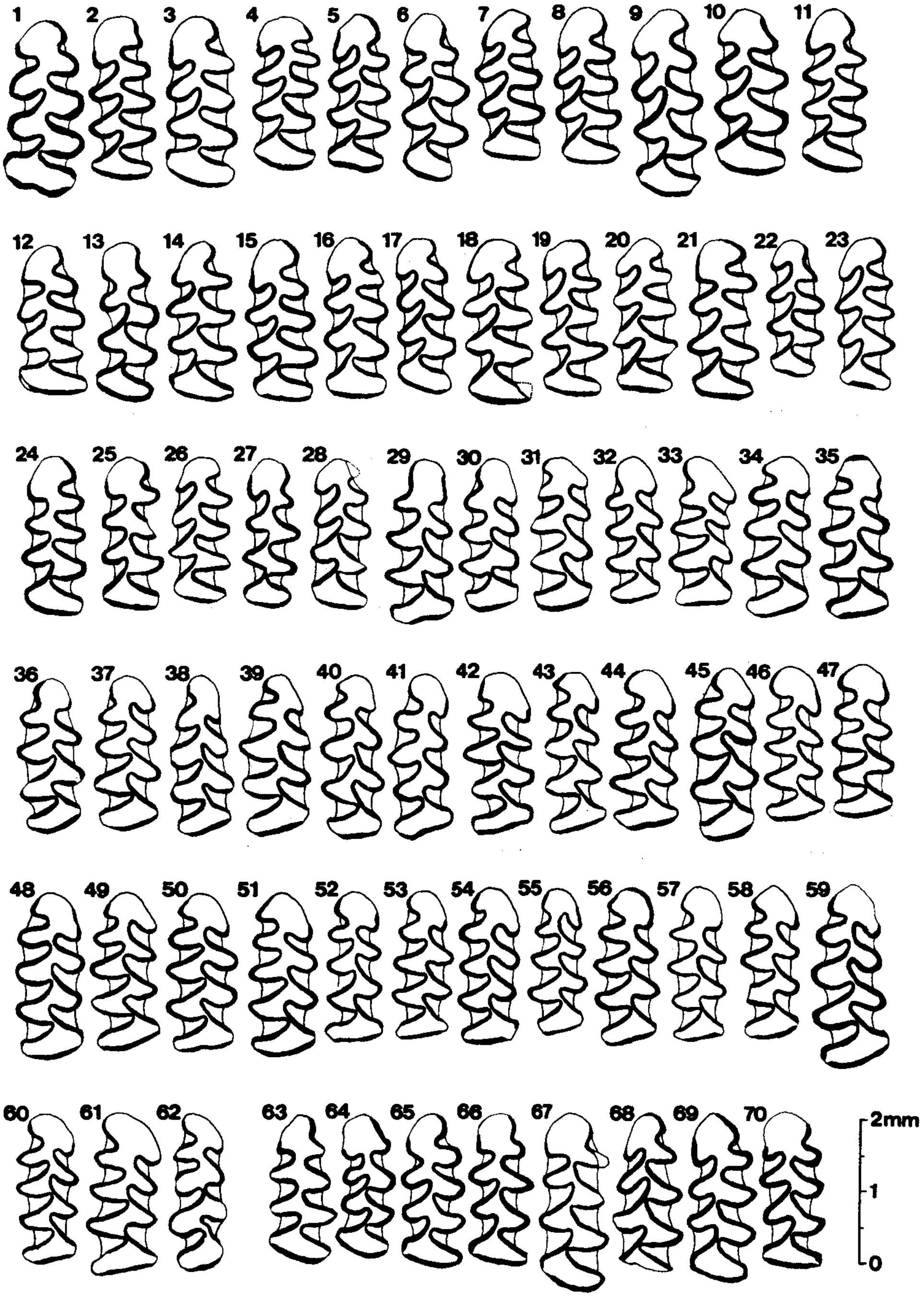
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Plate 17

***Clethrionomys-Phaulomys* transitional form**

Occlusal view of isolated M_1 without sign of root-formation.

1–14, left M_1 from F_1, F_2 and F_4 of Kumaishi-do Cave (*1,* YKS 00102; *2,* YKS 00106; *3,* YKS 00002; *4,* YKS 00020; *5,* YKS 00024; *6,* YKS 00041; *7,* YKS 00047; *8,* YKS 00050; *9,* YKS 00051; *10,* YKS 00052; *11,* YKS 00054; *12,* YKS 00076; *13,* YKS 00096; *14,* YKS 00099).

15–22, 24–28, 30–43, right M_1 from F_1, F_2 and F_4 of Kumaishi-do Cave (*15,* YKS 00017; *16,* YKS 00016; *17,* YKS 00030; *18,* YKS 00033; *19,* YKS 00045; *20,* YKS 00068; *21,* YKS 00090; *22,* YKS 00219; *24,* YKS 00059; *25,* YKS 00082; *26,* YKS 00223; *27,* YKS 00217; *28,* YKS 00001; *30,* YKS 00015; *31,* YKS 00046; *32,* YKS 00055; *33,* YKS 00060; *34,* YKS 00070; *35,* YKS 00086; *36,* YKS 00087; *37,* YKS 00092; *38,* YKS 00097; *39,* YKS 00103; *40,* YKS 00111; *41,* YKS 00112; *42,* YKS 00218; *43,* YKS 00220).

23, 29, right M_1 from Kumaishi-do Cave (site unknown). *23,* YKS 00003; *29,* YKS 00010.

44–50, left M_1 from F_8 of Kumaishi-do Cave (*44,* YKS 04052; *45,* YKS 04055; *46,* YKS 04056; *47,* YKS 04066; *48,* YKS 04068; *49,* YKS 04073; *50,* YKS 04074).

51–54, right M_1 from F_8 of Kumaishi-do Cave (*51,* YKS 04040; *52,* YKS 04044; *53,* YKS 04050; *54,* YKS 04067).

Plate 17

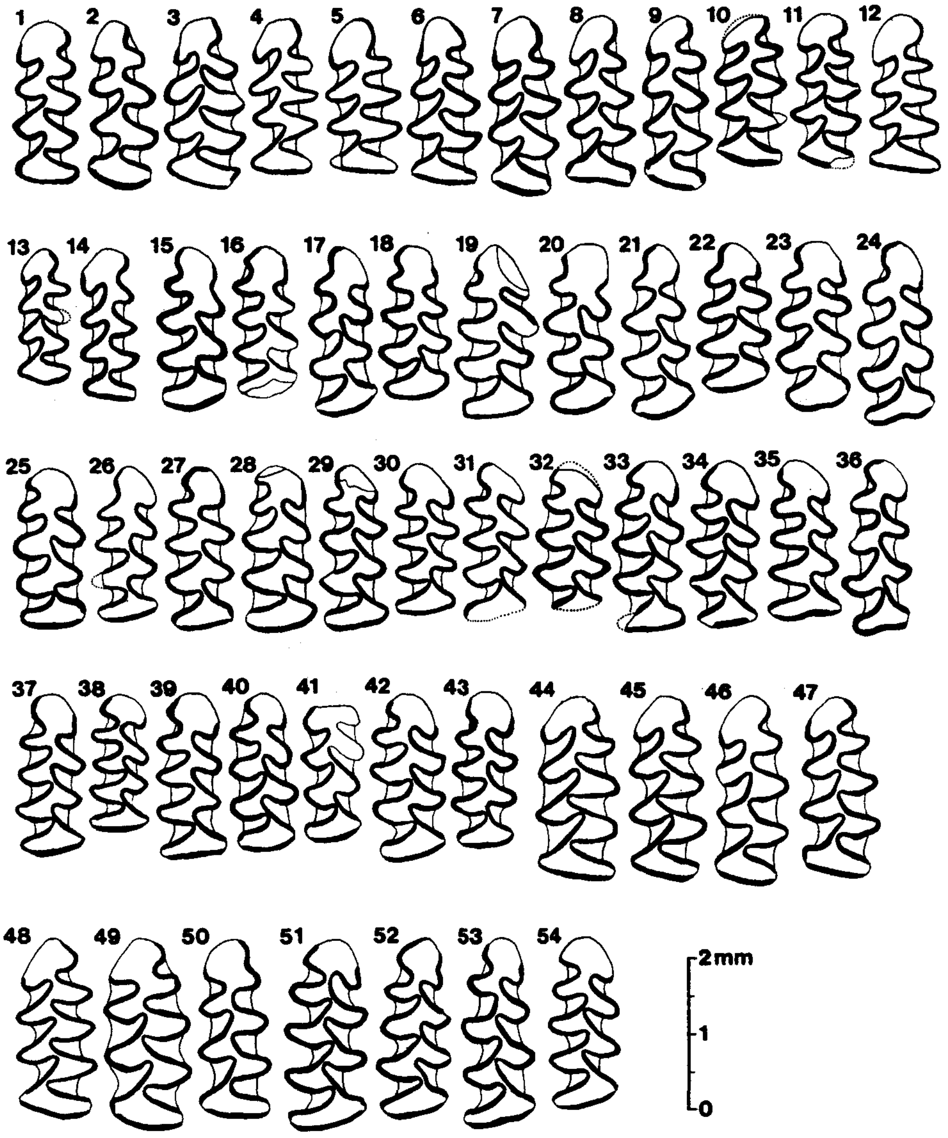
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Plate 18

Phaulomys cf. ***smithii***

Occlusal view of isolated M^3 (left M^3=*1–29, 44–48, 50–61, 67–77, 85*; right M^3=*30–43, 49, 62–66, 78–84*).

1–43, M^3 from the Late Pleistocene horizons of Kannondo Cave Site (*1*, HUA-K00711 from Horizon P; *2–8*, HUA-K00771 to 00777 respectively from the lower part of Horizon O; *9–11*, HUA-K02988, 02989 and 00918 respectively from the upper part of Horizon O; *12–25*, HUA-K02990 to 03003 respectively from the upper part of Horizon O; *26–29*, HUA-K00919 to 00922 respectively from the upper part of Horizon O; *30*, HUA-K00712 from Horizon P; *31–42*, HUA-K03004 to 03015 respectively from the upper part of Horizon O; *43*, HUA-K00923 from the upper part of Horizon O).

44–49, M^3 from Horizon V of Domen Cave Site (HUA-D00026 to 00031 respectively).

50–66, M^3 from Layer 2 of Tanuki-ana Cave (ASM 700756 to 700772 respectively).

67–84, M^3 from Husen-ana Cave (ASM 701170 to 701187 respectively).

85, M^3 from Ninjinkubo First Cave (Sotsuka Collection; unnumbered).

Plate 18

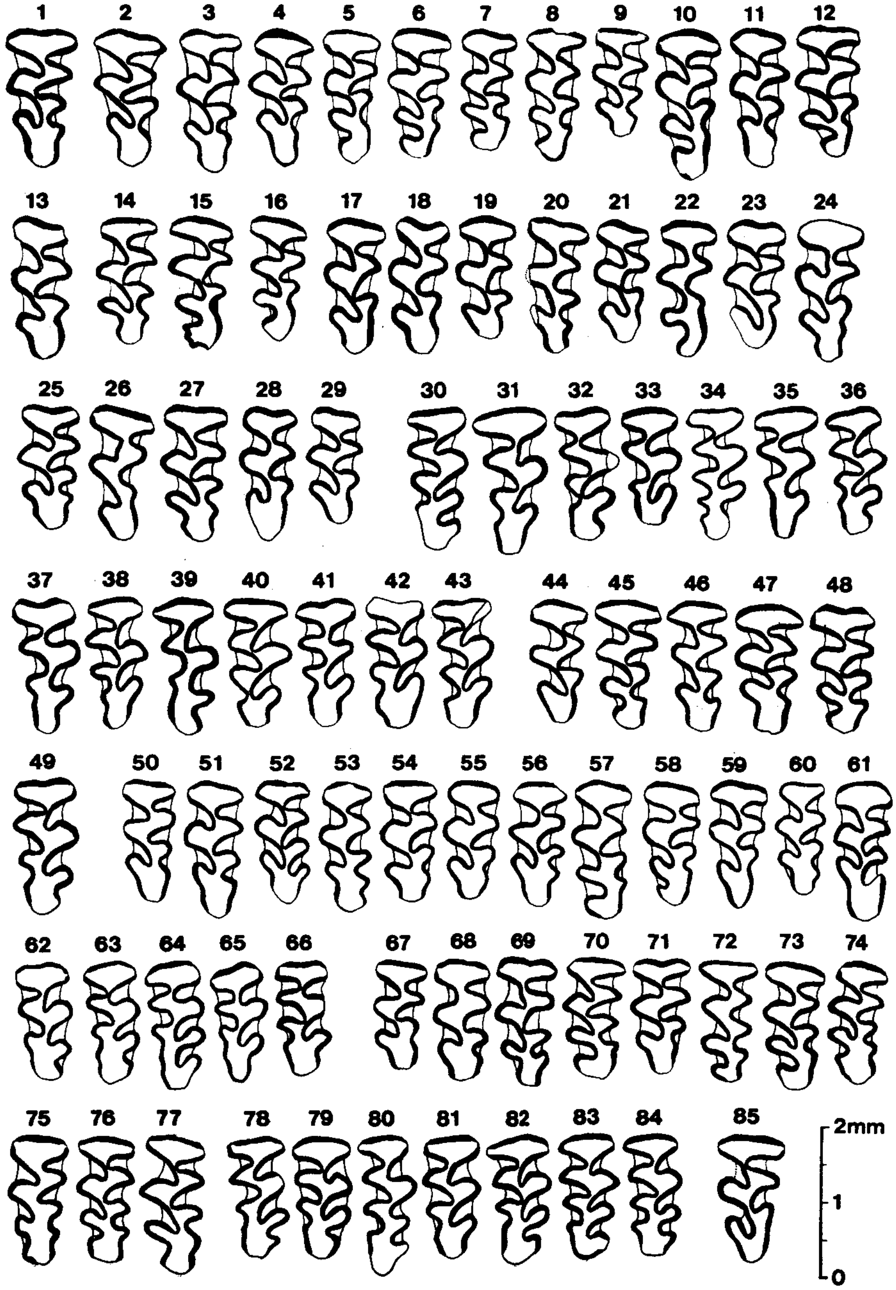
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Plate 19

Phaulomys cf. *smithii*

Occlusal view of M_1 (left M_1=*1–11*, *20–22*, *25–32*, *38–49*, *67–69*; right M_1=*12–19*, *23*, *24*, *33–37*, *50–66*, *70*, *71*).

1–24, M_1 from Kannondo Cave Site (*1*, HUA-K00719 from Horizon P; *2–8*, HUA-K00786 to 00792 respectively from the lower part of Horizon O; *9–11*, HUA-K00938 to 00940 respectively from the upper part of Horizon O; *12*, HUA-K00720 from Horizon P; *13–17*, HUA-K00793 to 00797 respectively from the lower part of Horizon O; *18*, *19*, HUA-K00941 and 00942 respectively from the upper part of Horizon O; *20*, HUA-K02946 from Horizon K; *21*, HUA-K02971 from Horizon H; *22*, HUA-K02962 from Horizon I; *23*, HUA-K03017 from Horizon I; *24*, HUA-K02976=horizon unknown).

25–37, M_1 from Layer 2 of Tanuki-ana Cave (*25*, ASM 700843; *26*, ASM 700844; *27*, ASM 700839; *28–36*, ASM 700845 to 700853 respectively; *37*, ASM 700838).

38–66, M_1 from Husen-ana Cave (ASM 701212 to 701240 respectively).

67–70, M_1 from Ninjinkubo First Cave (unnumbered specimens of the SOTSUKA Collection).

71, M_1 from Mejiro-do Cave (unnumbered specimen of the SOTSUKA Collection).

Plate 19

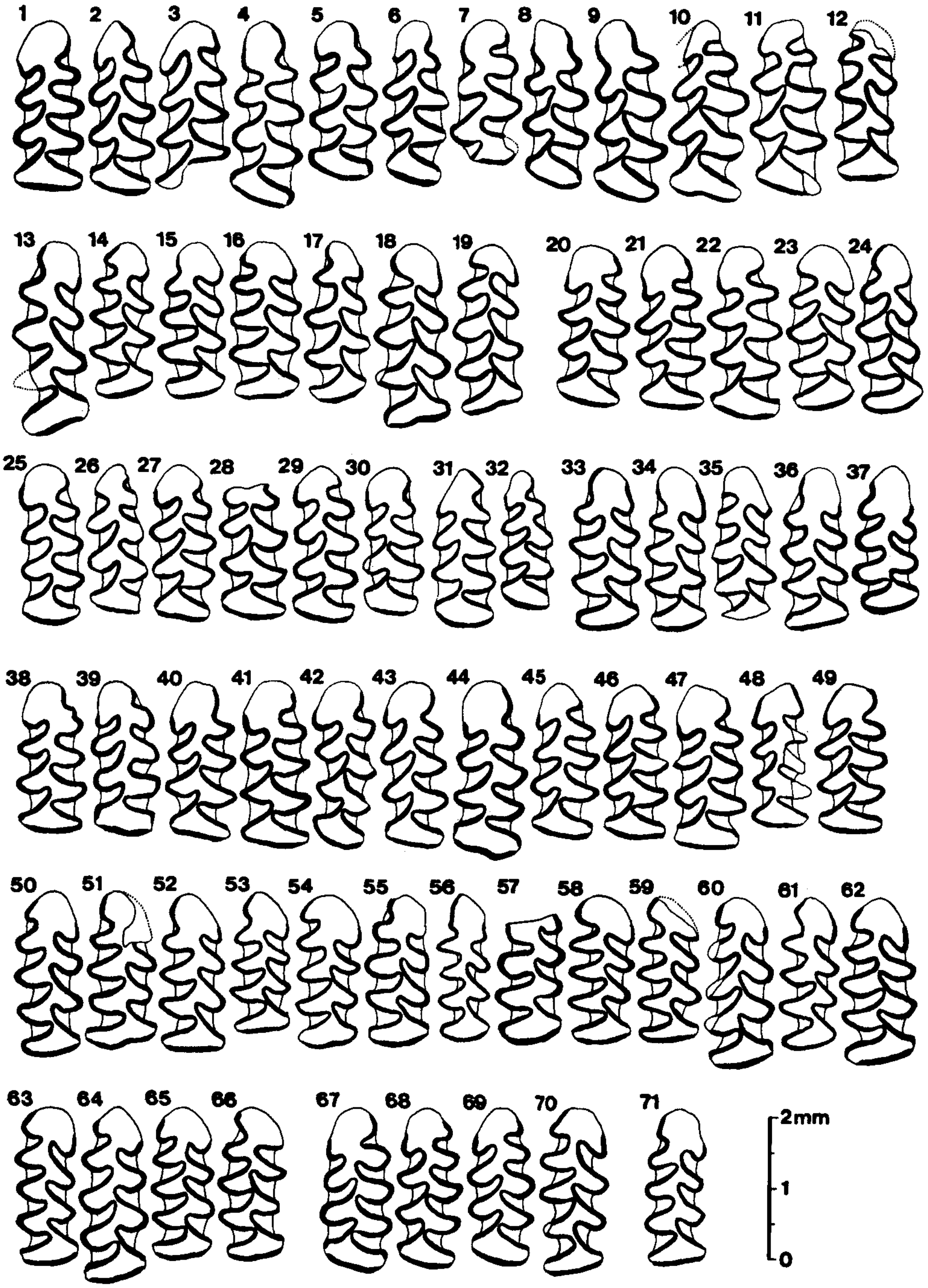
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Plate 20

Microtus montebelli

Lower tooth rows (*1–6, 9–12, 15, 16, 19*=left M_1 and M_2; *13*=right M_1, M_2 and M_3; *7, 8, 14, 17, 18, 20–25*=right M_1 and M_2).

1–8, specimens from Locality 3 of Ube Kosan Quarry (*1*, KUJC96230 from Layer 12; *2–4*, KUJC96200 to 96202 respectively from Layer 14; *5*, KUJC96184 from Layer 14; *6*, KUJC96076 from Layer 18; *7*, KUJC96232 from Layer 12; *8*, KUJC96208 from Layer 13).

9–14, unnumbered specimens from Yage Quarry (MATSUHASHI Collection). *9*, from Site 1; *10*, from Site 2; *11–13*, from Site 5; *14*, from Site 4.

15–17, specimens from the lower part of Horizon O of Kannondo Cave Site (*15*, HUA-K03075; *16*, HUA-K03074; *17*, HUA-K03076).

18, YKS 00291 from F_4 of Kumaishi-do Cave

19–23, specimens from Horizons I and J of Kannondo Cave Site (*19*, HUA-K03722 from Horizon I; *20*, HUA-K03716 from Horizon I; *21*, HUA-K03721 from Horizon I; *22*, HUA-K03719 from Horizon I; *23*, HUA-K03712 from Horizon J).

24, HUA-A00009 from Anagami Rockshelter Site.

25, ASM 701378 from Layer 2 of Tanuki-ana Cave.

Plate 20

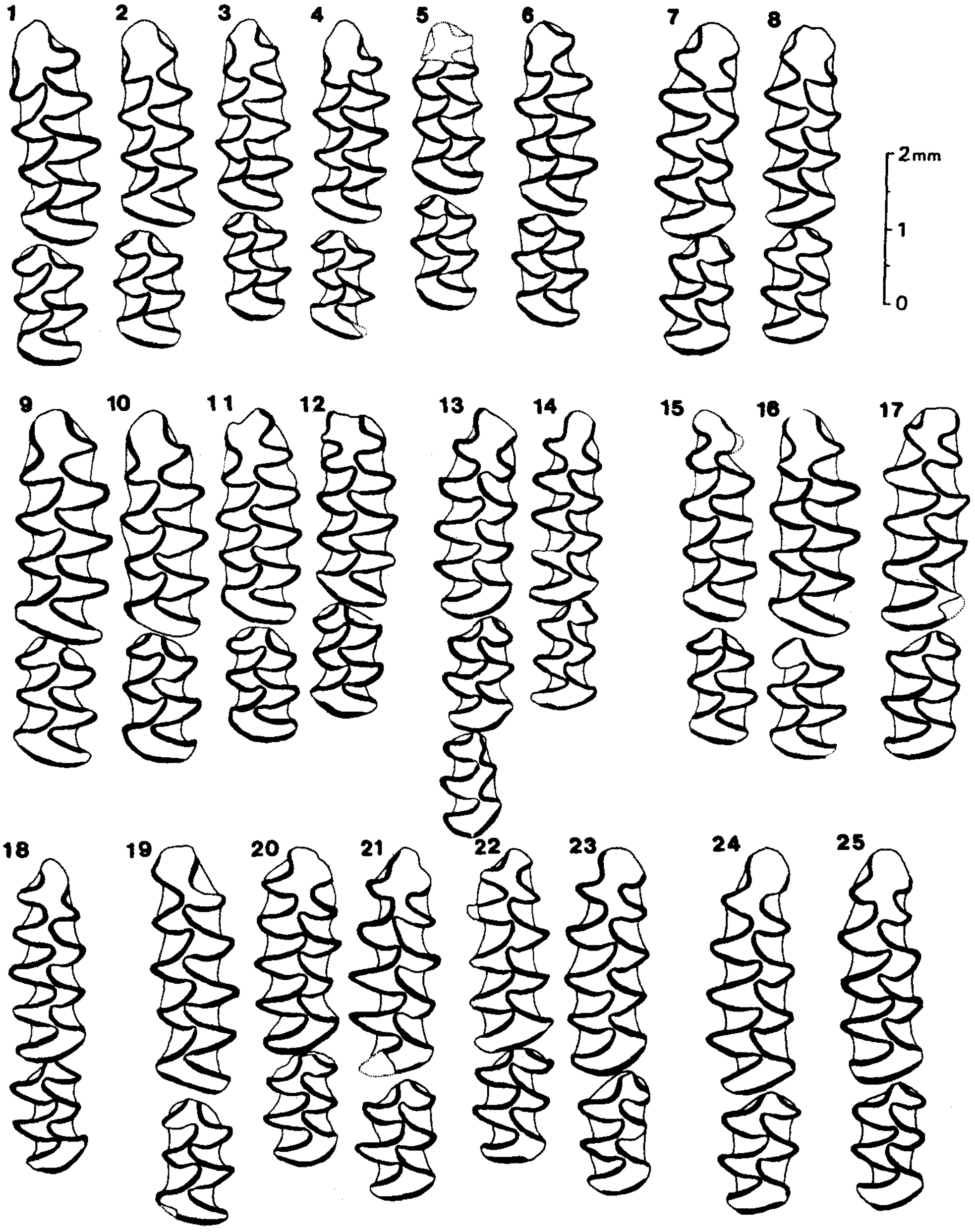

Plate 21

Microtus montebelli

Isolated M_1 with five closed triangles (left M_1=*1–16*, *36*, *37*, *39–48*; right M_1=*17–35*, *38*).

1–35, specimens from Locality 3 of Ube Kosan Quarry (*1*, KUJC96001 from Layer 1; *2*, *3*, KUJC96146 and 96147 respectively from Layer 8; *4*, *5*, KUJC96103 and 96104 respectively from Layer 10; *6*, KUJC96236 from Layer 12; *7–10*, KUJC96203, 96205, 96206 and 96207 respectively from Layer 13; *11–13*, KUJC96185, 96186 and 96187 respectively from Layer 14; *14–16*, KUJC96077, 96078 and 96079 respectively from Layer 18; *17–19*, KUJC96259, 96260 and 96261 respectively from Layer 6; *20*, *21*, KUJC96150 and 96151 respectively from Layer 8; *22*, KUJC96105 from Layer 10; *23–26*, KUJC96233, 96234, 96235 and 96209 respectively from Layer 12; *27*, KUJC96210 from Layer 13; *28–30*, KUJC96188, 96189 and 96190 respectively from Layer 14; *31*, *32*, KUJC96089 and 96090 respectively from Layer 17; *33*, KUJC96080 from Layer 18; *34*, KUJC96192 from Layer 14; *35*, KUJC96273=horizon unknown).

36–38, specimens from Layer 2 of Locality 1 of Ube Kosan Quarry (*36*, ASM 701303; *37*, ASM 701304; *38*, ASM 701305).

39–48, specimens from Sugi-ana Cave (KUJC100115 to 100124 respectively).

Plate 21

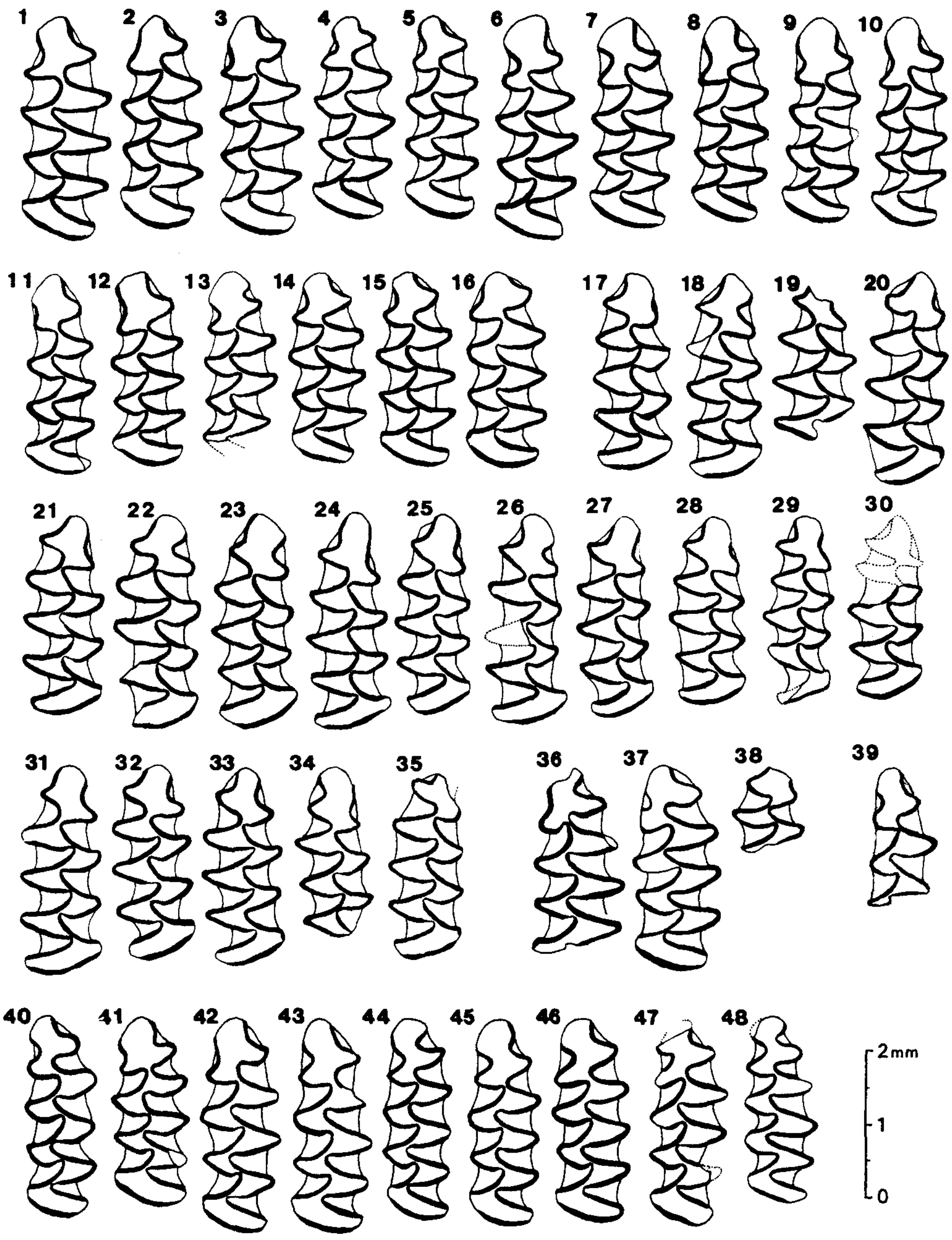
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Plate 22

Microtus montebelli

Isolated M_1 with five closed triangles (left M_1=*1*, *21–25*, *29–42*; right M_1=*2–20*, *26–28*, *43–47*).

1–20, KUJC100125 to 100144 respectively from Sugi-ana Cave.

21–23, specimens from Yage Quarry (*21*, unnumbered specimen of the MATSUHASHI Collection from Site 1; *22*, unnumbered specimen of the MATSUHASHI Collection from Site 5; *23*, KUJC100164 from Site 4-e).

24–28, KUJC100050 to 100054 respectively from Aisawa Quarry.

29–47, specimens from Kannondo Cave Site (*29–33*, HUA-K03154 to 03158 respectively from the upper part of Horizon O; *34–38*, HUA-K03077 to 03081 respectively from the lower part of Horizon O; *39*, HUA-K03794 from the lower part of Horizon O; *40–42*, HUA-K03083 to 03085 respectively from the lower part of Horizon O; *43–46*, HUA-K03159 to 03162 respectively from the upper part of Horizon O; *47*, HUA-K03086 from the lower part of Horizon O).

Plate 22

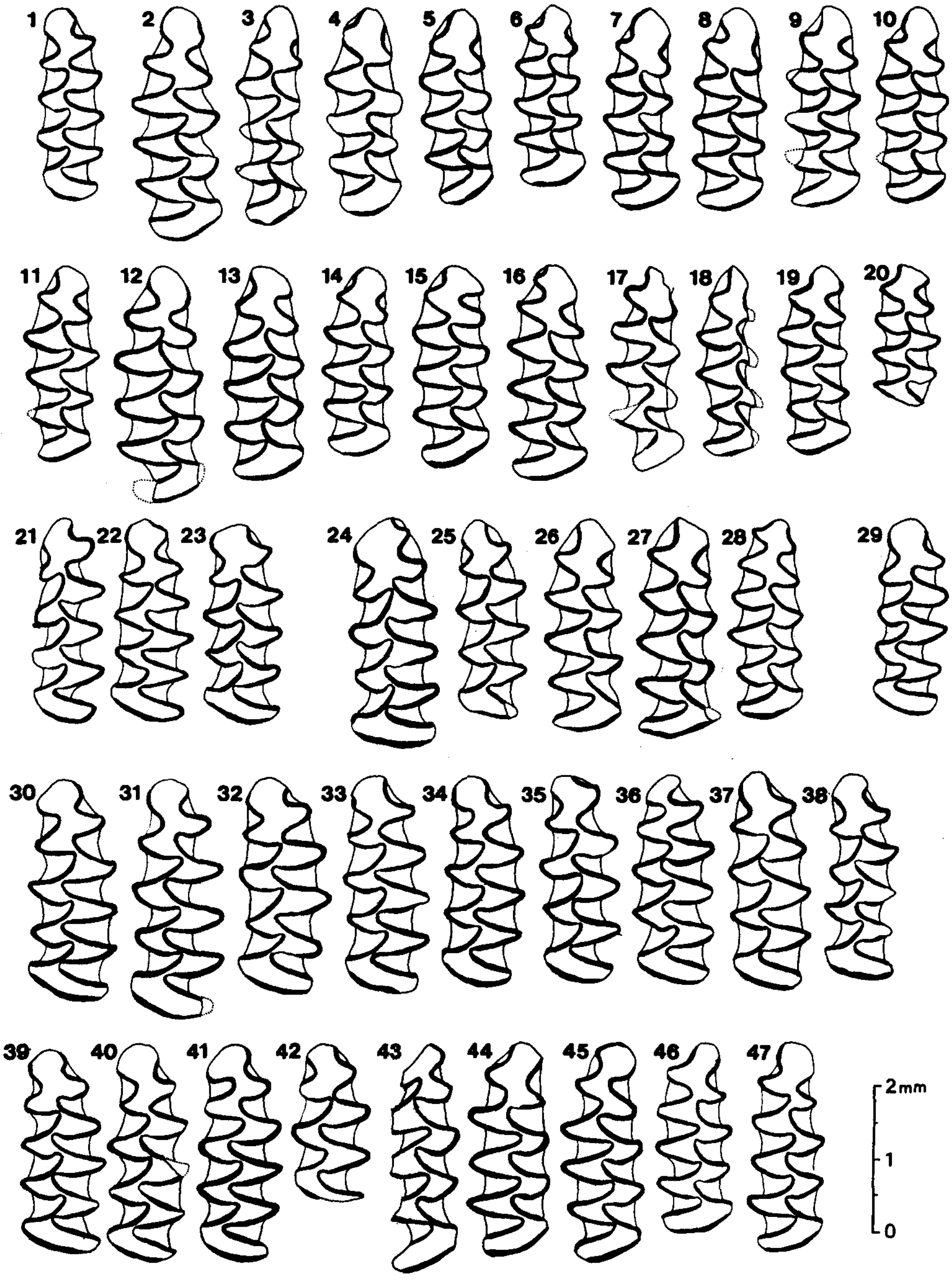
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Plate 23

Microtus montebelli

M_1 with five closed triangles (left M_1=*7–13*, *24–28*, *31–35*, *37*; right M_1=*1–6*, *14–23*, *29*, *30*, *36*, *38–40*).

1, HUA-K03087 from the lower part of Horizon O of Kannondo Cave Site; **2–6,** HUA-K03787 to 03791 respectively from the same horizon of the same site. **7–23,** specimens from Kumaishi-do Cave (YKS 00004, 00006, 00007, 00008, 00009, 00027, 00039, 00012, 00013, 00023, 00026, 00028, 00032, 00034, 00035, 00036 and 00038 respectively).

24–30, specimens from the Holocene horizons of Kannondo Cave Site (*24–27,* HUA-K03720, 03717, 03727 and 03723 respectively from Horizon I; *28,* HUA-K03710 from Horizon J; *29,* HUA-K03726 from Horizon I; *30,* HUA-K03713 from Horizon J).

31–36, ASM 701380 to 701385 respectively from Layer 2 of Tanuki-ana Cave.

37, ASM 701400 from Husen-ana Cave.

38, unnumbered specimen from Kitoragawa Site.

39, **40,** specimens with reduced LSA5 and/or BSA4 (morphotype R); *39,* ASM 701386 from Layer 2 of Tanuki-ana Cave; *40,* KUJC96191 from Layer 14 of Locality 3 of Ube Kosan Quarry (*40a,* occlusal view; *40b,* bottom view).

Plate 23

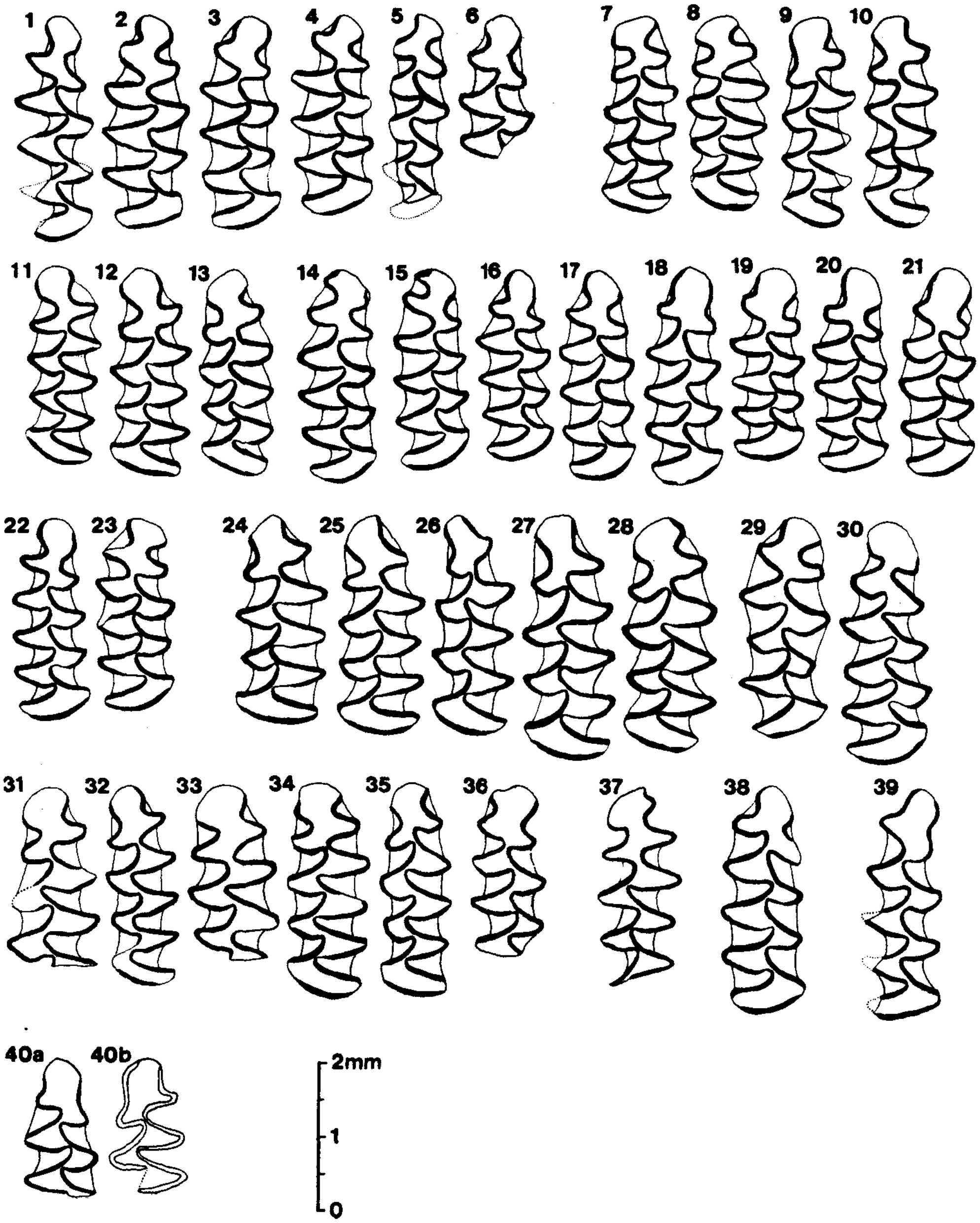
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Plate 24

Microtus epiratticepoides, sp. nov.

M_1 with broader Is 6 (isthmus index more than 3.0) from Locality 3 of Ube Kosan Quarry (*1–44*, left; *45–48*, right).

1–6, KUJC96003, 96007, 96009, 96010, 96021 and 96022 respectively from Layer 1; *7–11*, KUJC 96028, 96029, 96030, 96032 and 96035 respectively from Layer 2; *12*, KUJC96247 (horizon unknown); *13–16*, KUJC96039 to 96042 respectively from Layer 3; *17*, *18*, KUJC96056 and 96057 respectively from Layer 4; *19*, KUJC97139 from Layer 8; *20*, *21*, KUJC96253 and 96254 respectively from Layer 6; *22–24*, KUJC96135 to 96137 respectively from Layer 8; *25*, *26*, KUJC96113 and 96114 respectively from Layer 9; *27–29*, KUJC96099 to 96101 respectively from Layer 10; *30*, *31*, KUJC96246 and 96247 respectively from Layer 11; *32–34*, KUJC96225 to 96227 respectively from Layer 12; *35*, *36*, KUJC96198 and 96199 respectively from Layer 13; *37*, *38*, KUJC96177 and 96178 respectively from Layer 14; *39*, *40*, KUJC96134 and 96138 respectively from Layer 8; *41*, *42*, KUJC96075 and 96071 respectively from Layer 18; *43*, *44*, KUJC96270 and 96271 respectively (horizon unknown); *45*, KUJC 96004 from Layer 1; *46*, KUJC96072 from Layer 18; *47*, *48*, KUJC96005 and 96012 respectively from Layer 1.

Plate 24

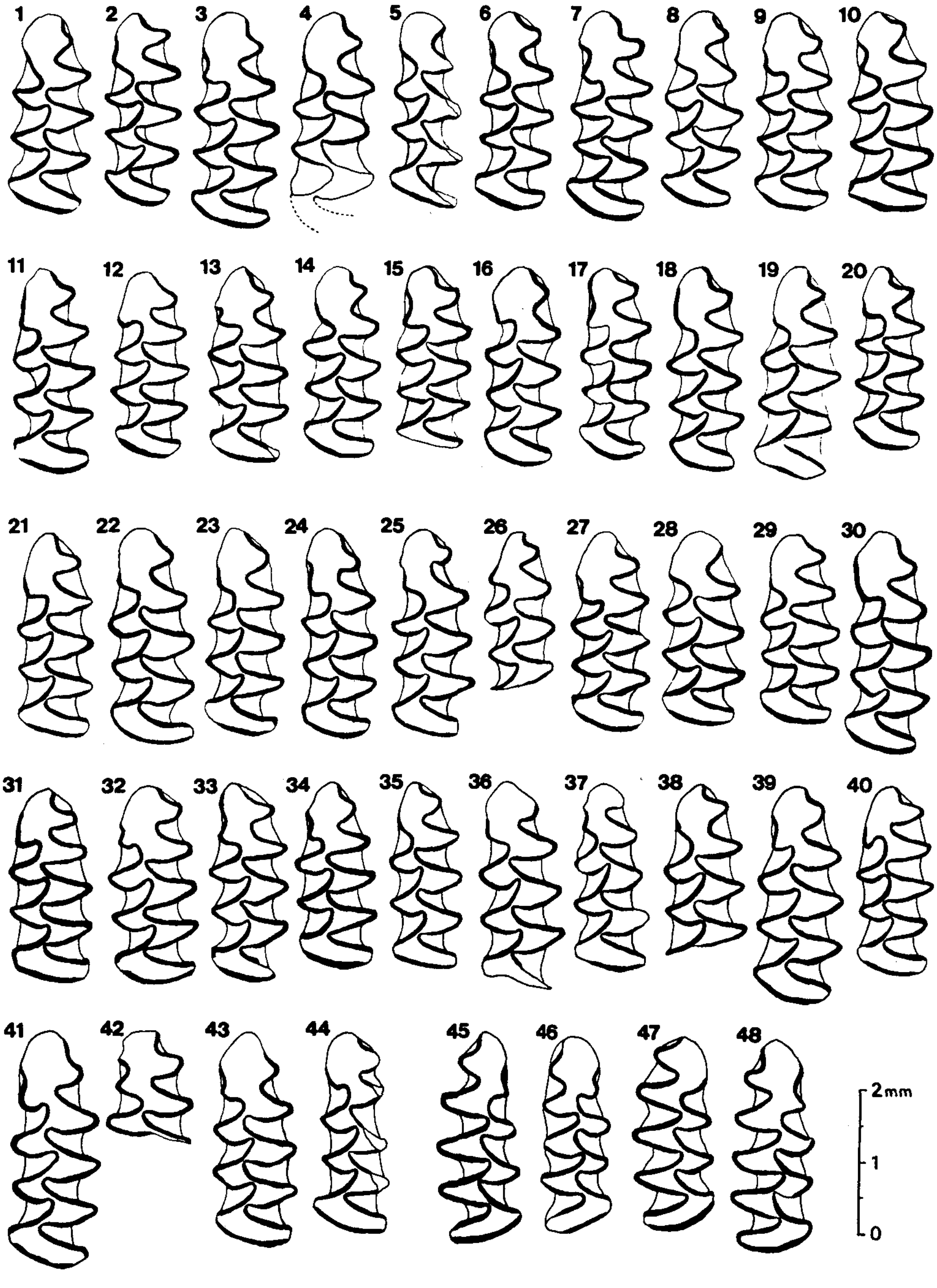
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Plate 25

Microtus epiratticepoides, sp. nov.

M_1 with broader Is 6 (isthmus index more than 3.0).

1–41, right M_1 from Locality 3 of Ube Kosan Quarry (*1–4*, KUJC96013 to 96016 respectively from Layer 1; *5*, KUJC96023 from Layer 1; *6*, *7*, KUJC96027 and 96036 respectively from Layer 2; *8–11*, KUJC96044 to 96047 respectively from Layer 3; *12*, *13*, KUJC96058 and 96059 from Layer 4; *14–17*, KUJC96255 to 96258 from Layer 6; *18–20*, KUJC96172 to 96174 from Layer 5; *21–26*, KUJC96140 to 96145 respectively from Layer 8; *27*, KUJC96112 from Layer 9; *28–32*, KUJC96115 to 96119 respectively from Layer 9; *33*, KUJC96102 from Layer 10; *34*, KUJC96229 from Layer 12; *35–39*, KUJC96179 to 96183 respectively from Layer 14; *40*, KUJC96098 from Layer 16; *41*, KUJC96120 from Layer 9).

42–48, left M_1 from Locality 1 of Ube Kosan Quarry (*42–46*, ASM 701409 to 701413 respectively from Layer 2; *47*, *48*, ASM 701404 and 701405 respectively from Layer 3b).

Plate 25

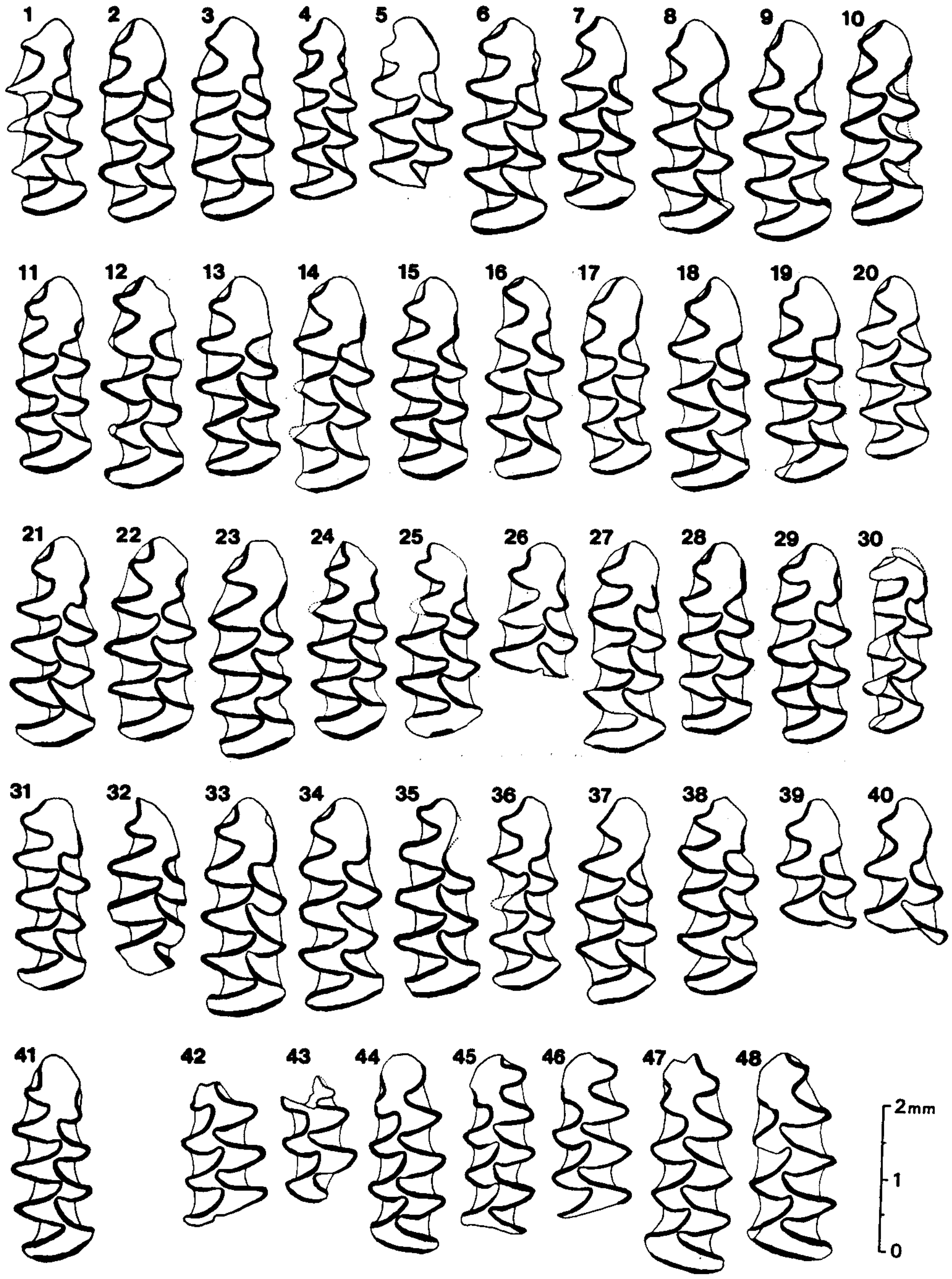
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Plate 26

Microtus epiratticepoides, sp. nov.

M_1 with broader Is 6 (isthmus index more than 3.0). right M_1=*1–5*, *15–21*, *27–33*, *35*; left M_1=*6–14*, *22–26*, *34*.

1–5, specimens from Locality 1 of Ube Kosan Quarry (*1*, ASM 701417 from Layer 1; *2–4*, ASM 701414 to 701416 respectively from Layer 2; *5*, ASM 701403 from Layer 4b).

6, ASM 701418 from Locality 2 of Ube Kosan Quarry.

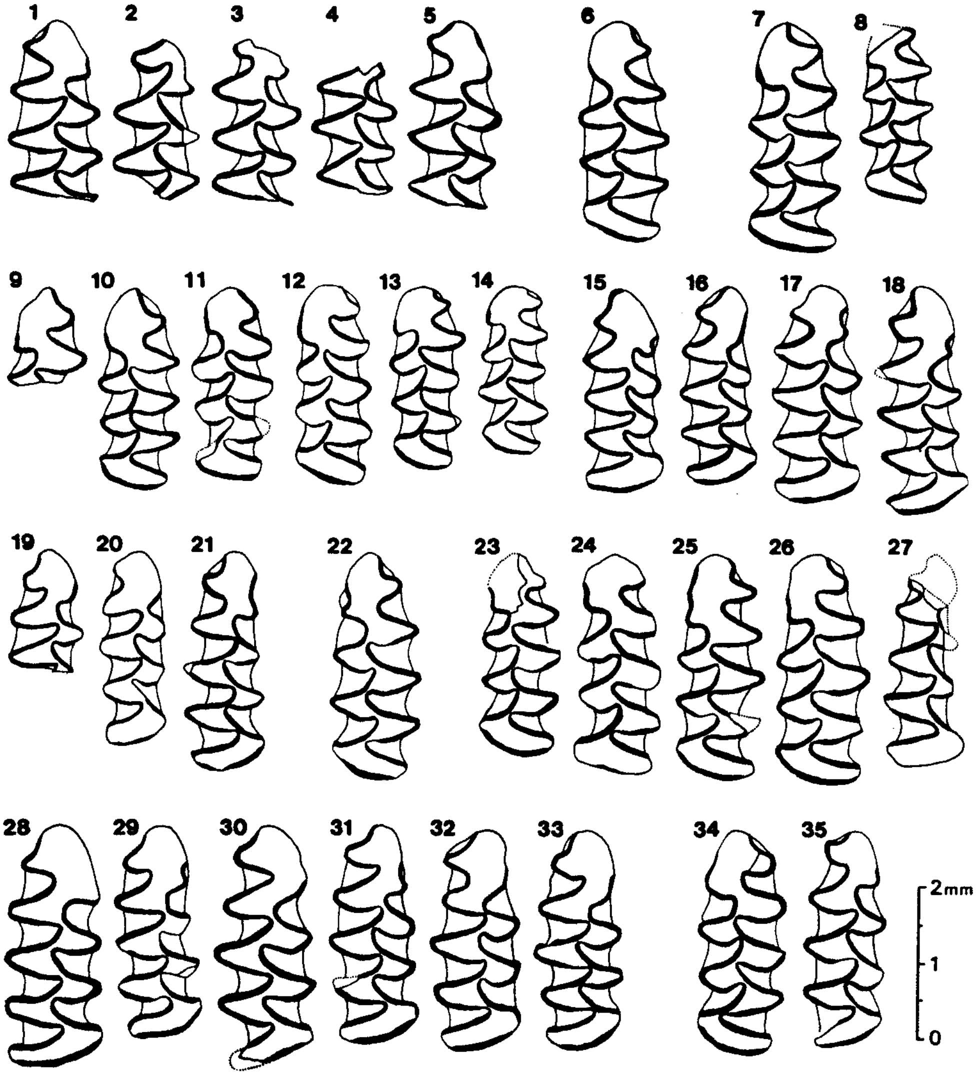
7–21, KUJC100170 to 100184 respectively from Sugi-ana Cave.

22, unnumbered specimen from Site 1 of Yage Quarry (MATSUHASHI Collection).

23–33, specimens from Kannondo Cave Site (*23*, *24*, HUA-K03729 and 03730 respectively from Horizon P; *25*, HUA-K03736 from the lower part of Horizon O; *26*, HUA-K03758 from the upper part of Horizon O; *27–31*, HUA-K03741, 03739, 03740, 03737 and 03738 respectively from the lower part of Horizon O; *32*, HUA-K03759 from the upper part of Horizon O; *33*, HUA-K03777 from Horizon N).

34, 35, YKS 00081 and 00085 respectively from F_4 of Kumaishi-do Cave.

Plate 26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