

Quaternary Rodent Faunas in the Japanese Islands (Part 1)

By

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Abstract

The results of the study on the rodent remains from the Japanese Quaternary are described and discussed. The remains comprise more than 10,000 specimens collected from 30 localities in Honshu, Kyushu and the Ryukyu Islands. Their systematic analysis results in the recognition of 18 forms including two new species, *Clethrionomys japonicus* and *Microtus epiratticepoides*. On the other hand, the fossiliferous sediments of those localities are examined precisely from the viewpoints of stratigraphy and geochronology. Based on these results, the following faunal succession is reconstructed.

From the Early Pleistocene to early Middle Pleistocene, the ancestors of living species migrated into the Honshu, Shikoku and Kyushu areas from various parts of the continent such as Europe, South Siberia, North and South China, and evolved into endemic species to those areas due to the influences of geographical isolation and adaptation to the characteristic temperate forest environments. Among those rodents, sciurids, murids and glirids have not changed in species level since the middle Middle Pleistocene, while arvicolids have taken on drastic changes with new immigrations. Namely, *Myopus schisticolor* appeared transiently in the middle Middle Pleistocene, and *Clethrionomys japonicus* underwent rapid divergence into *Phaulomys smithii* and *P. andersoni* from the late Middle to Late Pleistocene. Moreover, in the late Middle Pleistocene, *Microtus montebelli* appeared in the fauna as the last immigrant from the continent. This new arrival came to replace gradually the former inhabitants, *M. epiratticepoides* and *M. cf. brandtioides*, from the late Middle to Late Pleistocene. Finally, the last two forms were extinguished in those areas at the end of the Late Pleistocene. Apart from those families, cricetids appeared temporally in the middle Middle Pleistocene. As a whole, the exchange in rodent faunas between those areas and others (continen-

tal regions and Hokkaido) ceased in the late Middle Pleistocene, and never took place afterwards.

In the Ryukyu Islands, the Late Pleistocene and Holocene rodent faunas are represented by two endemic murids such as *Tokudaia osimensis* and *Diplothrix legata*. In spite of the opinions of the previous authors, the former possibly arose from the *Parapodemus-Apodemus* lineage in Pliocene, while the latter was probably originated from a primitive murid in Pliocene which was rather near to *Rattus* than to *Lenothrix* and *Lenomys*. They might flourish and have wide ranges in the islands until the Late Pleistocene, whereas their distribution was strongly reduced to restricted areas in Holocene.

I. Introduction

Among mammals, rodents are generally regarded as a successful group, because they are the richest in species number as well as in population. The Quaternary fossil records of this group are abundant and well investigated in Europe and North America, where the faunal succession and the evolutionary history of each taxon are adequately understood. Accordingly this group plays an important role for the Quaternary biostratigraphy in those areas.

The studies on the Quaternary rodents in Japan have far lagged behind those in Europe and North America. The first record of fossil rodents from the Quaternary sediments in Japan appeared in SHIKAMA's paper (1933), which has been followed by several papers dealing with these fossils. However most of these papers have provided only insufficient identification with no systematics. The only monographic treatment of the fossils was given by KOWALSKI and HASEGAWA (1976) who made systematic descriptions for the materials collected from various localities in Japan with brief discussion on the faunal succession. Because this work seems to be insufficient in variation analysis of population, specific identification of fossils and geochronological setting of fossiliferous sediments, its revision has been expected.

On the other hand, the studies on living rodents have been a main subject for Japanese mammalogists. Most of the rodents in the present Japanese Islands are represented by endemic forms in generic, specific or subspecific levels with a unique distribution pattern. Therefore the relationship with continental species and the origin of the rodent fauna have been a matter of debate. Nevertheless the fossil records have been usually ignored in the debates of the mammalogists. Therefore it is necessary to re-examine the debates from palaeontological viewpoints.

This paper aims to provide a monographic review of the Japanese Quaternary rodents with a revision of the previous works and some new ideas on the rodent faunal succession in the Japanese Islands. It includes the discussion on the origin of the species particular to the islands and their phylogenetic relationship with continental species.

In this paper, the stratigraphic sequences of the sediments yielding rodent fossils in Honshu, Kyushu and the Ryukyu Islands are described as precise as possible, and the whole mammalian faunas of the sediments are analysed numerically. Furthermore these sediments are correlated with each other by chronological data obtained by physico-chemical methods as well as the faunal characters of the mammals associated with rodents. On the other hand, more than ten thousand fossil specimens are systematically described. In order to confirm their accurate taxonomic position, the analysis of variation and morphological comparisons

with numerous living specimens were devoted. Moreover some of them were compared with the Chinese fossil specimens by the courtesy of the Institute of Vertebrate Palaeontology and Palaeoanthropology in Peking.

On the basis of all the results, the author tries to reconstruct comprehensively the faunal succession of the Quaternary rodents in the Japanese Islands as the conclusion of this paper. However the fossil records of rodents hitherto known from Japan are restricted to those in the later part of Quaternary. Therefore it cannot be denied that the present reconstruction of the faunal succession is still far from complete, but the author believes that it is the best interpretation of the knowledge hitherto obtained.

II. Historical Review

Although fossil rodents are abundantly contained in the Quaternary cave and fissure sediments in the Japanese Islands, no one in the palaeontologists paid attention to their significance before the publication of T. SHIKAMA's paper in 1933. In this paper, SHIKAMA dealt with the stratigraphy of the fossiliferous cave and fissure sediments exposed at several limestone quarries in Kuzuü, Tochigi Prefecture, which were named the "Kuzuü Formation." In the same paper, he provided the faunal lists of mammals obtained from the formation, in which four forms of rodents were included. In the subsequent paper (1937a), he revised the lists, and added the numerical analysis of the fauna.

In 1944, NAORA published a book dealing with the faunal history of the Japanese mammals, in which he listed several localities yielding fossil rodents. By his list, it was first clarified that these fossils occurred not only in Kuzuü but also in other areas of the Japanese territory at that time.

The Quaternary vertebrate fossils from the Kuzuü Formation were systematically described in SHIKAMA's monographic article (1949). However his descriptions of rodents were restricted to sciurids leaving other rodent families undescribed.

In the report of SHIKAMA *et al.* (1952) on the speleological survey of Same Cave, Shiga Prefecture, a faunal list of the fossiliferous sediments of the cave was provided. This list included three forms of rodents. Two years later, NAORA (1954) published a book titled "Old Stone Age in Japan," in which numerous fossil localities of the Quaternary mammals were described. Of these localities, he recorded rodent remains from eight localities in the Kuzuü Area and from Matsugae Cave, Kitakyushu, Fukuoka Prefecture, without systematic descriptions. In the same year, a new fossil locality was discovered in Shiriya Quarry, Shiryazaki, Aomori Prefecture. The mammalian fossils collected from this locality were subsequently reported by NAKAJIMA and KUWANO (1957) and NAKAJIMA (1958), and they recorded several forms of rodents in their faunal lists.

Since 1918, the Quaternary mammalian fossils have been occasionally found in cave and fissure sediments of various localities in the Akiyoshi Area, Yamaguchi Prefecture. Excepting a few preliminary reports, SHIKAMA and OKAFUJI's paper (1958) was the first attempt to establish the stratigraphy of these sediments and to describe the fossils from palaeontological

viewpoints. Although they listed several forms of rodents, they did not describe them systematically.

During four years subsequent to the publication of SHIKAMA and OKAFUJI's paper, the reports on the Quaternary mammals from three new localities appeared in scientific literatures. These localities are Ushikawa Mine, Toyohashi, Aichi Prefecture (SUZUKI and TAKAI, 1959), Tadaki Quarry, Mikkabi, Shizuoka Prefecture (TAKAI, 1962) and Shikimizu Quarry, Hijikawa, Ehime Prefecture (SHIKAMA and HASEGAWA, 1962). In these reports, either faunal lists or brief explanation of the mammals including several forms of rodents were provided.

The presence of exotic rodents* in the Quaternary sediments of Japan had been unknown, until HASEGAWA presented a faunal list of Ikumo Quarry (Ato, Yamaguchi Prefecture) in 1963. He recognized the remains of wood lemming, *Myopus*, in the fossiliferous sediments of this quarry. Three years later, the same author (1966) summarized the knowledge on the micro-mammalian faunas in the Japanese Quaternary obtained before 1966. In this paper, he newly provided the faunal lists of two important localities such as Ando Quarry in the Akiyoshi Area and Shiraiwa Mine, Inasa, Shizuoka Prefecture. Although he listed more than ten forms of rodents as a whole, their identification was insufficient from the current knowledge.

In 1968, HASEGAWA *et al.* reported vertebrate fossils from Ojika-do Cave and Hato-ana Cave on the Hirao-dai Plateau, Fukuoka Prefecture. In this paper, they listed two forms of rodents. Three years later, TAKAI and HASEGAWA (1971) briefly commented on the rodent remains collected from Minatogawa Site, Gushikami, Okinawa Prefecture. In 1972, NAORA described the mammalian remains including four forms of rodents from Shiriya Quarry which had been preliminarily reported by NAKAJIMA (1958). In the same year, KANEKO (1972) first pointed out the occurrence of an exotic vole* "*Microtus ratticeps*" in the fossil assemblage of Matsugae Cave which had been originally assigned to a living species, *M. montebelli*, by NAORA (1954).

In 1973, HASEGAWA *et al.* briefly described the rodent remains from Amagawa-do Cave and Tanabaru Cave in Miyako Island, Okinawa Prefecture, which were assigned to *Rattus* cf. *legata* (= *Diplothrix* cf. *legata*). This was the first record of *Diplothrix* in the southern part of the Ryukyu Islands where this genus is absent in the present day. In the next year, AIMI (1974) briefly mentioned the occurrence of two forms of rodents ("*Microtus ratticeps*" and *Clethrionomys* sp.) from the Middle Pleistocene sediments in the Akiyoshi Area. He regarded them as exotic forms* to the present Honshu.

The first monographic work on the Quaternary rodents from Japan was published by KOWALSKI and HASEGAWA (1976). They systematically described numerous materials from Shiriya Quarry, eight localities in the Kuzuü Area, Shiraiwa Mine, Ushikawa Mine, four localities in the Akiyoshi Area, Shikimizu Quarry, Hinigushiku (Okinawa Prefecture), Minatogawa Site, Amagawa-do Cave and Tanabaru Cave. They assigned these materials to 18 forms including two problematic species such as *Microtus epiratticeps* (= *M. ratticeps* of KANEKO, 1972

* A form which was already extinguished in one area, but still survives in another area is called "exotic form" to the former area in this paper.

and AIMI, 1974) and *Clethrionomys rufocanus* (= *C.* sp. of AIMI, 1974). Although this work is worth to be regarded as epoch-making, the description and classification of the rodent remains are not satisfactory for the present author. Moreover the age-determination for those fossil localities does not have good grounds. Therefore the interpretation on the faunal succession by those authors are not acceptable.

Since 1976, the Quaternary rodents of the Japanese Islands have been vigorously studied by several authors. These studies can be summarized as follows:

The occurrence of the rodent remains from Kannondo Cave Site in the Taishaku Area, Hiroshima Prefecture, was first mentioned by TANAKA (1976). On the other hand, KAWAMURA and ISHIDA (1976) reported the micro-mammalian fossils including several forms of rodents from Kumaishi-do Cave, Hachiman, Gifu Prefecture. The latter work was supplemented by KAWAMURA (1977a). However the systematic descriptions were not given in these papers.

In 1977, HASEGAWA *et al.* described the specimens of arvicolid remains from Ando Quarry which had not been described in KOWALSKI and HASEGAWA (1976). However the taxonomic conclusion of these authors was not always coincident with that of KOWALSKI and HASEGAWA. In the same year, KAWAMURA (1977b) described a molar of *Cricetulus* from Sumitomo Quarry in the Akiyoshi Area. This was the first discovery of fossil hamster in Japan. According to him, the climate of those days might have been more continental than in the present day.

In 1978, KAWAMURA published a preliminary report on the micro-mammalian remains from Kannondo Cave Site which included a number of rodent remains. This report was followed by a series of works by the same author (KAWAMURA, 1979a, 1980, 1981, 1982; KAWAMURA *et al.*, 1986). These works revealed that this site was the most important fossil locality for reconstructing the faunal succession of rodents from the Late Pleistocene to Holocene in Japan. On the other hand, TOMIDA (1978), HASEGAWA and NOHARA (1978) and HASEGAWA *et al.* (1978) briefly mentioned the occurrence of rodent remains from Yage Quarry, Inasa, Shizuoka Prefecture, from Ishisukuyama, Ishigaki Island, Okinawa Prefecture and from Gohezu Cave, Ie Island, Okinawa Prefecture, respectively.

In 1979, KAWAMURA (1979b) discussed the faunal succession of micro-mammals since the Late Pleistocene on the basis of the stratigraphic relationship among various fossil localities in Japan. Additionally, KAWAMURA and FOSSIL MAMMAL RESEARCH GROUP OF NOJIRI-KO EXCAVATION (1979) described the Late Pleistocene rodent remains from the Nojiri-ko Formation. This was the first record of the Pleistocene rodents from lacustrine sediments in Japan. In the next year, the reports on the mammalian remains from three localities were successively published. They are KAWAMURA and TAMIYA (1980) on Tanuki-ana Cave in the Akiyoshi Area, KAWAMURA and KAJIURA (1980) on Sugi-ana Cave, Hachiman, Gifu Prefecture and MIYAO *et al.* (1980) on Tochibara Rockshelter Site, Kitaaki, Nagano Prefecture. Although these authors listed various forms of rodents in each locality, their systematic descriptions were not given except two extinct or exotic arvicolids from Sugi-ana Cave.

In 1981, MIYAO *et al.* published a biometrical study on the lower molars of *Apodemus speciosus* from Tochibara Rockshelter Site. On the other hand, KAWAMURA (1983) identified the vertebrate remains from Anagami Rockshelter Site in the Taishaku Area, and made the

numerical analysis of the remains. He also recognized four species of rodents in spite of their scarce occurrence. In the next year, KAWAMURA and SOTSUKA (1984) reported the mammalian remains collected from eight caves on the Hirao-dai Plateau, which included several forms of rodents. Additionally, MIYAO (1984) briefly mentioned the occurrence of rodent remains from Miwa Cave, Minokamo, Gifu Prefecture.

In 1985, HACHIYA *et al.* reported the results of the biometrical analysis for the molars of *Apodemus* collected from Ando Quarry. In the same year, the report on the excavation of Pinza-Abu Cave in Miyako Island, Okinawa Prefecture, was published. This report contained two papers on rodent remains (HASEGAWA, 1985 and KANEKO, 1985). The latter paper was important, because it dealt with the remains of *Microtus* which had been unknown from the Quaternary of the Ryukyu Islands.

III. Materials and Methods

A. Fossil materials

More than ten thousand specimens are examined in the present study. Almost all of them are taxonomically described in Chapter VII. However few specimens which were already described in the previous papers of the present author are excluded from the descriptions of that chapter. The localities which yielded the examined materials are listed below (see Fig. 1: Abbreviations in parenthesis indicate the geological ages of the fossiliferous sediments of each locality; namely MP=Middle Pleistocene, LP=Late Pleistocene, H=Holocene).

1. Kuzuü

Aisawa Quarry (LP): Formally called "Aisawa Quarry of Nittetsu Kogyo Co.," Aisawa, Kuzuü-cho, Aso-gun, Tochigi Prefecture.

2. Nojiri-ko (Lake Nojiri)

Nojiri-ko Formation (LP): Bottom of Lake Nojiri, Tategahana, Shinano-machi, Kamiminouchi-gun, Nagano Prefecture.

3. Gujohachiman

3-1. Kumaishi-do Cave (LP): Kumaishi, Miyama, Hachiman-cho, Gujo-gun, Gifu Prefecture.

3-2. Sugi-ana Cave (LP): Higashi-akuda, Hachiman-cho, Gujo-gun, Gifu Prefecture.

4. Yage

Yage Quarry (LP, MP): Formally called "Kawai Sekkai Quarry," Yage, Inasa-cho, Inasa-gun, Shizuoka Prefecture.

5. Suse

Suse Quarry (LP, H): Formally called "Suse First Mine of Mitake Mining Co.," Yumaki, Suse-cho, Toyohashi, Aichi Prefecture.

6. Higashiosaka

Kitoragawa Site (H): Yayoi-cho, Higashi-osaka, Osaka Prefecture.

7. Taishaku

7-1. Domen Cave Site (H): Shimotani, Kamitoyomatsu, Toyomatsu-mura, Jinseki-gun, Hiroshima Prefecture.

7-2. Anagami Rockshelter Site (H): Seto, Shinmen, Yuki-cho, Jinseki-gun, Hiroshima Prefecture.

7-3. Kannondo Cave Site (LP, H): Nagano, Jinseki-cho, Jinseki-gun, Hiroshima Prefecture.

8. Ikumo

Ikumo Quarry (MP): Formally called "Okamura Sekkai Quarry," west of Nakamura, Ikumo,

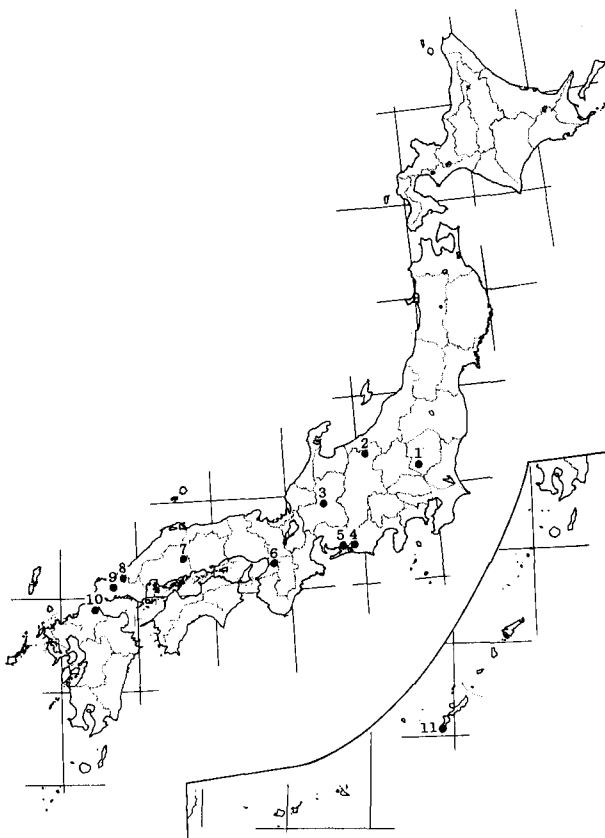


Fig. 1. Distribution of the fossil localities studied in this paper.

1, Kuzuū; 2, Nojiri-ko; 3, Gujohachiman; 4, Yage; 5, Suse; 6, Higashi-osaka; 7, Taishaku; 8, Ikumo; 9, Akiyoshi; 10, Hirao-dai; 11, Okinawa.

Ato-cho, Abu-gun, Yamaguchi Prefecture.

9. **Akiyoshi**

- 9-1. Tanuki-ana Cave (H): East of Wakatake-yama, Akiyoshi-dai, Shuho-cho, Mine-gun, Yamaguchi Prefecture.
- 9-2. Husen-ana Cave (H): North of Hirotani, Shuho-cho, Mine-gun, Yamaguchi Prefecture.
- 9-3. Sumitomo Quarry (MP): Formally called "Shuho Mine of Sumitomo Cement Co.," Minamidai, Shuho-cho, Mine-gun, Yamaguchi Prefecture.
- 9-4. Ube Kosan Quarry (MP, LP): Formally called "Quarry of Isa Cement Plant of Ube Kosan Co.," Isa-cho, Mine, Yamaguchi Prefecture.

10. **Hirao-dai** (all localities are situated on Hirao-dai, Kokuraminami-ku, Kitakyushu, Fukuoka Prefecture).

- 10-1. Seiryukutsu Cave (LP).
- 10-2. Hirao-ana Cave (H).
- 10-3. Ohera-ana Cave (H).
- 10-4. Ninjinkubo First Cave (H).
- 10-5. Yakubono-ana Cave (H).
- 10-6. Mejiro-do Cave (LP).

- 10-7. Ojika-do Cave (H).
- 10-8. Oiwa-ana Cave (H).
- 10-9. Yoshigatani Third Cave (H).

11. Okinawa

- 11-1. Kuteken (LP): Kuteken, Chinen-son, Shimajiri-gun, Okinawa Prefecture.
- 11-2. Minatogawa Site (LP, H): Minatogawa, Gushikami-son, Shimajiri-gun, Okinawa Prefecture.
- 11-3. Iso (LP): Iso, Urasoe, Okinawa Prefecture.
- 11-4. Gajanbira (LP): Kakihana-cho, Naha, Okinawa Prefecture.

All the materials except private collections have been housed in the following universities and institutions, after this study was finished:

1. Department of Geology and Mineralogy, Faculty of Science, Kyoto University (prefix for registered specimens=**KUJC**): The materials from Aisawa Quarry, Sugi-ana Cave, Yage Quarry (in part), Locality 3 of Ube Kosan Quarry (most specimens of this locality), Kuteken, Minatogawa Site, Iso and Gajanbira (most specimens).
2. Akiyoshi-dai Museum of Natural History (the prefix=**ASM**): The materials from Ikumo Quarry, Tanuki-ana Cave, Husen-ana Cave, Sumitomo Quarry, Localities 1, 2, and 4 of Ube Kosan Quarry, and Locality 3 of the same quarry (in part).
3. Department of Archaeology, Faculty of Letters, Hiroshima University (the prefix=**HUA**): The materials from Domen Cave Site, Anagami Rockshelter Site and Kannondo Cave Site.
4. Kitakyushu Museum of Natural History (the prefix=**KMNH VP**): The materials from Seiryukutsu Cave.
5. Association for the Preservation of the Archaeological Sites, Higashi-osaka City: The materials from Kitoragawa Site.
6. Nojiri-ko Museum: The materials from the Nojiri-ko Formation.
7. Department of Earth Sciences, Aichi University of Education: The materials from Kumaishi-do Cave are provisionally stored there. Most of them are numbered with the prefix **YKS** (Yoshinari KAWAMURA's provisional specimen number).

The following private collections were also examined in the present study:

1. Takashi SOTSUKA's Collection: The materials from Hirao-ana Cave, Ohera-ana Cave, Ninjin-kubo First Cave, Yakubono-ana Cave, Mejiro-do Cave, Ojika-do Cave, Oiwa-ana Cave and Yoshigatani Third Cave.
2. Yoshitaka MATSUHASHI's Collection: The materials from Yage Quarry (in part) and Suse Quarry.
3. Itsuro OSHIRO's Collection: The materials from Gajanbira (in part).

B. Recent comparative materials

More than a thousand recent specimens are examined for the comparisons with the present fossil materials. Most of them are stored in the Department of Earth Sciences, Aichi University of Education. They were collected from the following localities (Fig. 2):

1. Koshimizu: Koshimizu-cho, Shari-gun, Hokkaido.
2. Nopporo: Nopporo, Atsubetsu-cho, Shiroishi-ku, Sapporo, Hokkaido.
3. Tonden: Tonden-cho, Kita-ku, Sapporo, Hokkaido.
4. Otaki: Otaki-mura, Usu-gun, Hokkaido.
5. Noboribetsu: Noboribetsu-onsen, Noboribetsu, Hokkaido.
6. Karumai: Karumai-cho, Kunohe-gun, Iwate Prefecture.
7. Miyako: Miyako, Iwate Prefecture.
8. Sugaya: Takine-cho, Tamura-gun, Fukushima Prefecture.

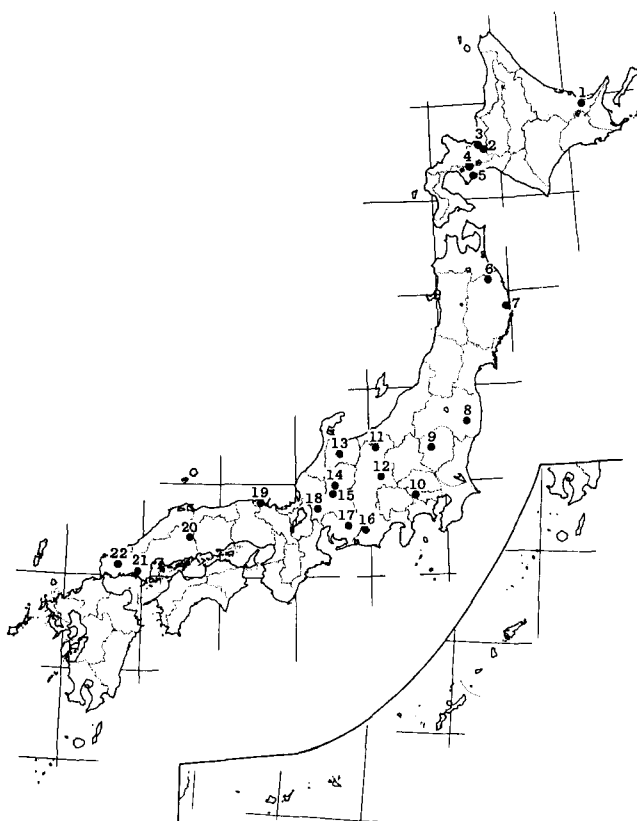


Fig. 2. Distribution of the localities from which the recent materials were collected.

1, Koshimizu; 2, Nopporo; 3, Tonden; 4, Otaki; 5, Noboribetsu; 6, Karumai; 7, Miyako; 8, Sugaya; 9, Nikko; 10, Mt. Takao; 11, Nojiri-ko; 12, Mt. Yatsugadake; 13, Kurehayama; 14, Myogata; 15, Gujohachiman; 16, Sakuma; 17, Mikawa Heights; 18, Ikeda; 19, Mineyama; 20, Taishaku; 21, Tokuyama; 22, Akiyoshi.

9. Nikko: Nikko, Tochigi Prefecture.
10. Mt. Takao: Takao-san, Hachioji, Tokyo Prefecture.
11. Nojiri-ko: Shinano-machi, Kamiminouchi-gun, Nagano Prefecture.
12. Mt. Yatsugadake: Maruyama, border area between Chino and Yachiho-mura, Nagano Prefecture.
13. Kurehayama: Toyama, Toyama Prefecture.
14. Myogata: Myogata-mura, Gujo-gun, Gifu Prefecture.
15. Gujohachiman: Miyama, Hachiman-cho, Gujo-gun, Gifu Prefecture.
16. Sakuma: Sakuma-cho, Iwata-gun, Shizuoka Prefecture.
17. Mikawa Heights: Inabu-cho, Shidara-cho and Toyota, Aichi Prefecture.
18. Ikeda: Ikeda-cho, Ibi-gun, Gifu Prefecture.
19. Mineyama: Mineyama-cho, Naka-gun, Kyoto Prefecture.
20. Taishaku: Kamitaishaku, Tojo-cho, Hiba-gun, Hiroshima Prefecture.
21. Tokuyama: Nakazu, Tokuyama, Yamaguchi Prefecture.
22. Akiyoshi: Akiyoshi-dai, Shuho-cho, Mine-gun, Yamaguchi Prefecture.

In addition to these, the following private and university collections are also examined:

1. Collection of the Department of Anatomy, School of Dentistry, Aichi-Gakuin University: Sciurids and glirids from several localities of Nagano Prefecture, and murids from Amami-oshima (Kagoshima Prefecture).
2. Masaomi KANAMORI's private collection: Arvicolids and murids from Sugadaira (Nagano Prefecture) and Korea.
3. Mitoshi TOKUDA's private collection: Cricetids, arvicolids and murids from England and China.
4. Mitsuru AIMI's private collection: Arvicolids from Mt. Chokai (Yamagata Prefecture), Mt. Yatsugadake (Nagano Pref.) and Mt. Tsurugi (Tokushima Pref.).
5. Shigeki WATANABE's private collection: Murids from Aokigahara (Yamanashi Prefecture).
6. Tsuneaki KOBAYASHI's private collection: Arvicolids and murids from several localities of Hokkaido, and from USSR and China.
7. Yumiko NAKAISHI's private collection: Murids from Nagoya (Aichi Prefecture).

C. Collecting method for fossil materials

Washing and screening of sediments are effective for collecting micro-vertebrate fossils. Many previous palaeontologists have attempted to apply them to various kinds of sediments with various geological ages. The technique of the washing and screening was summarily explained by HIBBARD (1949) and McKENNA (1965), but their explanations are not always suitable for the Japanese Quaternary sediments which yield micro-vertebrate fossils (mainly fissure and cave deposits). Therefore the present author devised his own method, and successfully obtained numerous micro-vertebrate fossils. The procedure of this method is summarized as follows:

1) Sampling of large quantities of sediments: Unweathered sediments were collected from each layer of the examined localities. Their weights were recorded in order to estimate the ratio of fossil contents.

2) Dissolution of the sediments: It is not always easy to screen raw sediments. Peculiar treatments are often requested for the dissolution of the sediments. In Japan, the fossiliferous fissure and cave sediments are mostly sticky clay or brecciated clay. These sediments were generally dissolved by the action of H_2O_2 . In case of hard travertine, weak acetic acid was effective (less than 10%). When this acid was applied, the sediments were sufficiently washed in water or neutralized by alkalis, after the dissolution.

3) Screen-washing: The dissolved sediments were washed in running water by a screen with a 0.5 mm mesh. From the experience of the present author, this mesh size is most appropriate for collecting micro-vertebrate fossils in Japan.

4) Drying and sorting: The residues on the screen were dried up without any artificial heating. After dried, they were roughly screened by coarser screens (for example, 5 mm and 3 mm meshes) to sort into several grades. Such sorting makes the next procedure easy.

5) Hand picking: All fossil bones and teeth contained in the sorted sediments were picked out with the naked eye, or by means of magnifier or binocular microscope.

This method was completely applied to adequate amount of sediments (more than 100 kg) in the following localities: Kumaishi-do Cave, Kitoragawa Site, Domen Cave Site, Late Pleistocene horizons of Kannondo Cave Site, Tanuki-ana Cave, and Localities 1 and 3 of Ube Kosan Quarry. On the other hand, the application of this method was incomplete or the quantity of the sediments was insufficient (less than 100 kg) in the following localities: Aisawa Quarry, Yage Quarry (in part), Anagami Rockshelter Site, Sumitomo Quarry, Localities 2 and

4 of Ube Kosan Quarry, Seiryukutsu Cave and the four localities of Okinawa.

The specimens from the following localities were collected directly at each outcrop, or by other screening methods (less accurate methods): Nojiri-ko Formation, Sugi-ana Cave, Suse Quarry, Holocene horizons of Kannondo Cave Site, Ikumo Quarry, Husen-ana Cave and all examined caves on Hirao-dai except Seiryukutsu Cave.

D. Dating methods

In the Japanese Islands, almost all the rodent fossils are obtained from cave and fissure sediments. The stratigraphic sequence of these sediments are generally complicated with difficulties in their geochronological estimation. Moreover, because each fissure and cave can be regarded as an independent sedimentary basin, their mutual correlations are further difficult. However, in order to reconstruct the faunal succession, it is inevitable to describe the sediments of each locality precisely with accurate dates and to correlate reasonably with each other. It is ideal that the age of each sediment is determined by physico-chemical and stratigraphic methods other than biological ones to avoid logical inconsistency, when the faunal succession is discussed. However the sediments examined here are not always in the reach of these dating methods. In this circumstance, the characters of mammalian fauna in association with rodents are utilized to determine the biostratigraphic position of the sediments as a subsidiary method. Accordingly the methods used here are divided into "non-faunal" ones (physico-chemical, tephrochronological and archaeological methods) and faunal ones, and briefly explained below.

1. Non-faunal methods

Because the dating by non-faunal methods was carried out mainly by other researchers and institutions, the details of the methods are not described here.

Radiocarbon dating —

^{14}C dates of collagen extracted from fossil bones were newly determined for the samples collected from Site 5 of Yage Quarry, East Fissure of Suse Quarry and Layer 4 of Tanuki-ana Cave at Gakushuin University. Other ^{14}C dates appeared in this paper are cited from other papers.

Uranium-series dating —

Fragments of travertine and fossil bones collected from Locality 3 of Ube Kosan Quarry, Ikumo Quarry and Sumitomo Quarry were dated by the U-series method by K. KOMURA and T. HAYASHI (pers. comm.). Because bones are not ideal closed-system in comparison with travertine, their dates are interpreted as minimum ages.

Amino-acid racemization dating —

The amino-acid dates of fossil bones shown in Table 17 are determined by S. MATSU'URA (pers. comm.). This method is applicable to absolute dating in local scale, when calibration samples are available and thermal histories of analysed samples can be inferred.

Uranium content in fossil bones —

The uranium contents shown in Table 17 are analysed by K. KOMURA and T. HAYASHI (pers. comm.). They provide the relative age within one area, when the geological conditions

of the fossil localities are identical with or similar to each other. Because uranium is saturated in fossil bones later than fluorine, it can be considered that uranium is a better time-indicator than fluorine in the samples with earlier geological ages.

Fluorine content —

The fluorine contents shown in Table 17 are analysed by S. MATSU'URA (mostly personal communication, but partly published in MATSU'URA, 1984). They also indicate the relative age of fossil bones which are collected from the localities with identical or similar geological conditions within one area.

Tephrochronology —

Numerous volcanic ash layers intercalated in the Quaternary sediments of the Japanese Islands are well investigated and dated. Some of them can be utilized for the age determination of the fossiliferous sediments examined here. They are the Kanuma Pumice Bed in the Kuzuü Area, the Ukinuno Pumice-fall Bed and AT Volcanic Ash Layer in the Taishaku Area, and the Aso-4 Pyroclastic Flow in the Akiyoshi Area (see the descriptions of each fossil locality in Chapter IV).

Archaeological dating —

When potteries and other artifacts are obtained from fossiliferous sediments, the relative age of the sediments can be determined by using them as time-indicator. In the present paper, the results of the researches on Anagami, Domen, Kannondo and Kitoragawa Sites by the archaeologists of Hiroshima University and the Association for the Preservation of Archaeological Sites, Higashi-osaka City are cited.

Fossilization —

Detailed observation of fossil bones sometimes provides information on their antiquity. However its application to dating should be limited to the case that the data by other non-faunal methods are not available because of the paucity of objectivity.

2. Faunal methods

In the present paper, the characters of mammalian fauna except rodents are utilized for relative dating of the sediments, when the non-faunal methods are insufficiently applied or their application is impossible. The occurrences of the large mammals whose biostratigraphic ranges were already determined are especially useful.

Ratio of extinct forms plus exotic ones to Japan in associated fauna —

This ratio is generally higher in earlier periods but lower in later ones. Therefore it provides the relative age of the sediments. In this paper, it is used for dating in the case that the fauna comprises a number of taxa (at least eight forms) belonging to various orders including micro-mammals.

Occurrence of elephants —

The ranges of *Stegodon orientalis* and *Palaeoloxodon naumanni* are considered to be 0.6 to 0.3 m.y. and 0.3 to 0.017 m.y. in the Japanese Islands (KAMEI and SETOGUCHI, 1970; KAMEI, 1984). On the other hand, the Holocene sediments yield no proboscideans. The occurrences of those species indicate that the sediments are assignable to the above-mentioned ranges.

Occurrences of rhinocerotids and giant deer —

Although the rhinocerotids from the Japanese Quaternary were quite insufficiently studied by the previous authors, their occurrences seem to be restricted to the Middle Pleistocene. On the other hand, YABE's giant deer, *Sinomegaceros yabei*, is exclusively known from the Middle and Late Pleistocene sediments in Japan. Its last appearance is presumably dated as ca. 10,000 yr. B.P. Therefore the occurrences of these mammals are significant from biostratigraphic viewpoints. Their stratigraphic ranges will be discussed in a separate paper.

Occurrences of boar and deer —

As already pointed out by KAWAMURA (1980), *Sus scrofa* is absent or quite rare in the Late Pleistocene sediments of Honshu, Shikoku and Kyushu, while it is abundantly found in the Holocene sediments of the same area. Therefore the mode of occurrence of this species has biostratigraphic significance for the sediments of these periods, when adequate specimens are available. This problem will be discussed in a separate paper on the basis of sufficient data.

In the Ryukyu Islands, HASEGAWA (1980a) noticed the stratigraphic distribution of *Sus* and cervids. Namely only cervids are found in the Late Pleistocene sediments, while they are coexistent with *Sus* in the Latest Pleistocene. Moreover *Sus* exclusively occurs in the Holocene sediments, although artifacts made of cervid bones are rarely found in the archaeological sites of this period. Therefore the coexistence of *Sus* and cervids suggests that the sediments are of latest Pleistocene age.

Mode of occurrence of Anourosorex japonicus —

This extinct insectivore species is abundantly found in the Middle Pleistocene sediments, but is scarce in the Late Pleistocene ones. Moreover the time of its extinction is considered to be about 18,000 to 14,000 yr. B.P. Therefore the mode of its occurrence provides a criterion for the dating of the fossiliferous sediments. The details will be discussed separately.

E. Spelling of scientific name

With regard to the spelling of species-group names based on male personal names, CORBET (1984) noted that the original spelling was to be retained without omitting the second "i," when the names ended in "ii" (see Article 33, *International Code of Zoological Nomenclature* 1985). Such a treatment is followed in the present paper (for example, *Miniopterus schreibersii* and *Phaulomys smithii* instead of *Miniopterus schreibersi* and *Phaulomys smithi* respectively).

IV. Geology of Fossil Localities

A. Middle Pleistocene localities

1. Ikumo Quarry

Ikumo Quarry is located at the south-eastern corner of the Palaeozoic "Zomeki Limestone Mass." This quarry was formally called "Okamura Sekkai Quarry," which had been worked during the period about from 1926 to 1965. In the later half of this period, fossil bones were occasionally found in cave or fissure sediments exposed on quarry faces. The vertebrate fauna of these sediments was first preliminarily reported by HASEGAWA and HARA (1962). Subse-

quently HASEGAWA (1963, 1966) provided more complete faunal lists and briefly discussed the characters of the fauna. But unfortunately, systematic descriptions of these fossils have been hitherto unpublished except rodent remains*.

In October 1979, the author had an opportunity to visit this quarry with the guidance of H. OKAMURA, the owner of this quarry. At this time, they could find neither fossil bones nor fossiliferous sediments there. But fortunately, by courtesy of H. OKAMURA, the author could examine his private collection which had been collected from the fossiliferous sediments of the quarry and preserved in his house for more than 15 years**. This collection contains many taxa of vertebrates, but mammalian fossils are exclusively described in this paper.

The fossiliferous sediments of this quarry are quite insufficiently recorded by the previous authors. KAWANO and TAKAHASI (1966) briefly mentioned these sediments in their study on the Quaternary lacustrine and fluvial deposits in the Tokusa Basin near this quarry. According to them, the following sequence was observed in the sediments of the quarry in descending order:

Red brecciated clay ca. 1 m (in thickness)
 Yellowish brown clay..... ca. 0.4 m
 Grey gravelly sand..... 0.4 m +

As KAWANO and TAKAHASI stated, it seems to be impossible to correlate these sediments with terrace deposits in the neighbouring area. However the sediments can be considered as the

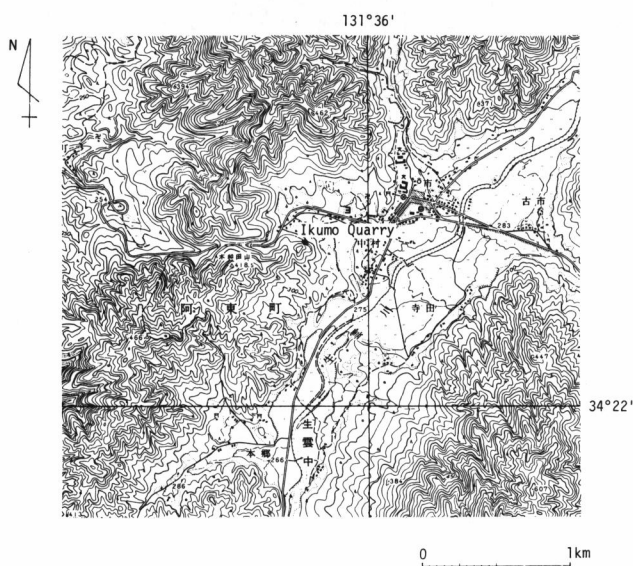


Fig. 3. Index map showing the location of Ikumo Quarry. The scale 1:25,000 map sheet "Ikumonaka" published by the Geographical Survey Institute is used.

* The rodents were described by KOWALSKI and HASEGAWA (1976).

** His collection is now stored in the Akiyoshi-dai Museum of Natural History.

Middle Pleistocene in age from the results of U-series dating and fluorine test of the fossil bones as well as from the faunal evidences discussed in Chapter VI of this paper.

2. Sumitomo Quarry

Akiyoshi-dai, the largest karst plateau in Japan, is composed of the Early Carboniferous to Late Permian limestone called the Akiyoshi Limestone Group. This plateau is topographically divided into the eastern part (Akiyoshi-dai in narrow sense) and western part (Nishi-akiyoshi-dai) by the valley of the Koto River running from north to south. Sumitomo Quarry (=Shuho Mine of Sumitomo Cement Company) is situated at the northeastern corner of Nishi-akiyoshi-dai.

In 1969, T. KURAMOTO and H. NAKAMURA, zoologists of the Akiyoshi-dai Museum of Natural History, found a fossiliferous fissure exposed on a quarry face in the southern part of this quarry (Fig. 4). The fissure was filled with reddish brown clay which was partly changed into hard travertine. Numerous bones and teeth of bats were contained in the clay, but fossils of other mammals were very rare. Soon after the discovery, the fissure was completely destroyed by the limestone quarrying. But fortunately, by the effort of G. OKAFUJI, the

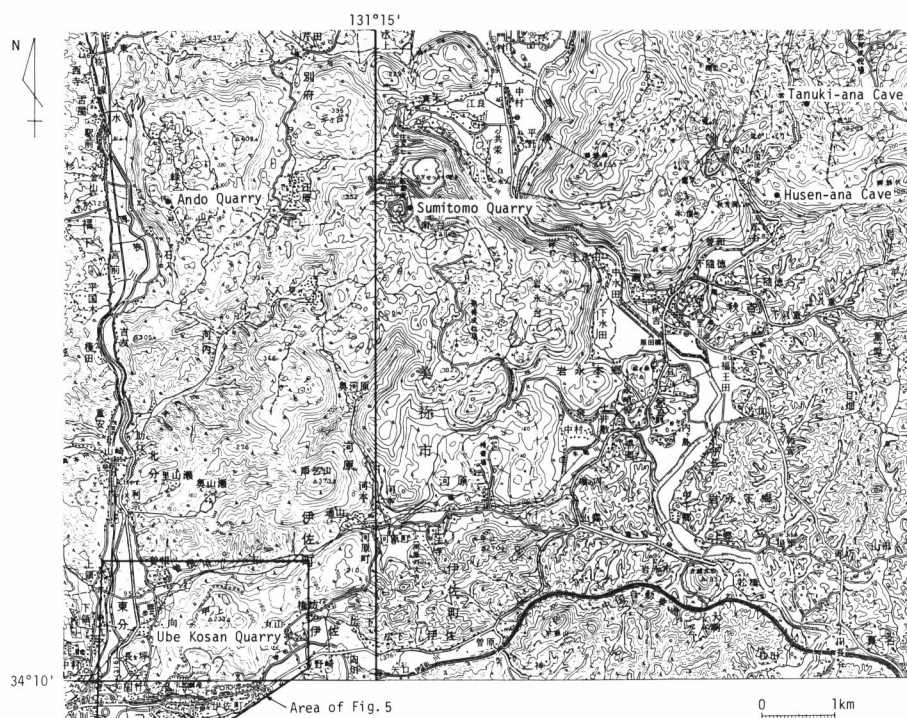


Fig. 4. Index map showing the locations of Tanuki-ana Cave, Husen-ana Cave, Sumitomo Quarry (exact position of the fossiliferous fissure), Ando Quarry and Ube Kosan Quarry. The area including the last quarry is shown in more detail in Fig. 5. The scale 1:50,000 map sheets "Yamaguchi," "Nishiichi" and "Asa" published by the Geographical Survey Institute are used.

sediments were partly transported to another place in the quarry, and were saved from the subsequent destruction for several years.

In May 1976, the author visited this site, and collected a number of fossiliferous travertine blocks. Some of these blocks were dissolved by the action of weak acetic acid, and then screened to extract micro-mammalian fossils. Although the fossil mammals from this locality were already studied by other authors (KOWALSKI and HASEGAWA, 1976; HASEGAWA, 1980b; YOON *et al.*, 1984), some additional knowledge was obtained by the investigation of these fossils. In Chapter V, the faunal characters of this locality will be discussed on the basis of all the works.

OKAFUJI *et al.* (1977) and YOON *et al.* (1984) briefly described the present fissure and its sediments, but these descriptions are insufficient from stratigraphic viewpoint. Moreover the visit of the present author was too late to observe them directly. Therefore the stratigraphic sequence of the sediments is, unfortunately, left unknown. However the U-series dating and faunal composition suggest that the sediments are Middle Pleistocene in age as discussed in Chapter VI.

3. Ube Kosan Quarry

The name "Ube Kosan Quarry" is an abbreviation for the limestone quarry of Isa Cement Plant of Ube Kosan Company*. This quarry is one of the largest limestone quarries in Japan, which covers almost all the area of a hilly mountain immediately north of a town of Isa (Figs. 4 and 5). This mountain is composed mainly of the Akiyoshi Limestone Group. On its southeastern slope, there are small limestone quarries mined by two different companies such as Nippon Sekkai Co. and Yakusen Sekkai Co.

In these quarries, vertebrate fossils have been occasionally discovered in cave and fissure sediments exposed on quarry faces. The first description of these fossils by SHIKAMA and TAKAHASHI appeared in 1949, which dealt with the materials from Fifth Quarry of Nippon Sekkai Co. In 1958, SHIKAMA and OKAFUJI published a more extensive work on the Quaternary cave and fissure deposits and their fossils in the Akiyoshi Area which included Ube Kosan Quarry as well as the quarries of Nippon Sekkai Co. In the same year, additional large mammalian fossils were discovered in Ube Kosan Quarry. These fossils were subsequently assigned to *Stegodon* and *Panthera* by SHIKAMA and OKAFUJI (1963) who emphasized their biostratigraphic significance. Moreover the occurrences of fossil elephants from the same quarry in 1961, 1966 and 1969 were recorded by OKAFUJI (1971).

Before 1977, palaeontologists paid little attention to the occurrence of micro-mammalian fossils from Ube Kosan Quarry. From 1977 to 1978, fossiliferous cave and fissure sediments were found to expose on the quarry faces at four localities in this quarry. These localities were named Localities 1 to 4 in order of discovery. The investigation by the present author demonstrated that these sediments contained rich micro-mammalian fossils. Of these localities, Localities 1, 3 and 4 are described here, because their sediments are considered to be Middle Pleistocene in age.

* SHIKAMA and OKAFUJI (1958) called it "Quarry of Ube Kosan Company."

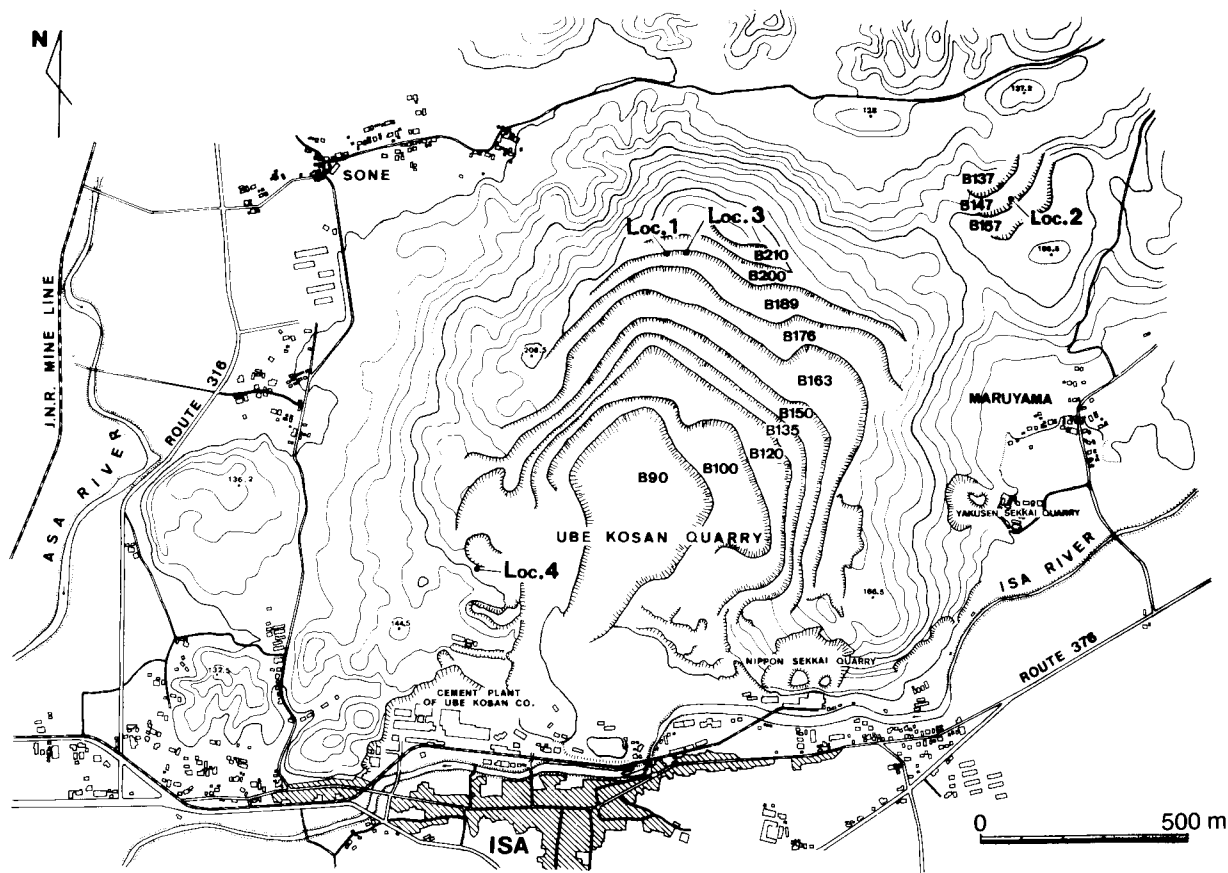


Fig. 5. Detailed map of Ube Kosan Quarry showing the locations of the four fossil localities (Loc. 1–4) and quarrying benches (B90–210) in 1978. The number of each bench indicates its elevation above sea level (for example, B90=bench of 90 m above sea level).

Locality 1 —

Because the company has employed “bench-cut technique” for limestone mining in recent years, a number of terraces called “bench” are formed in the quarry. Each bench is named by its height above sea level (for example, bench of 90 m etc.; see Fig. 5). From 1977 to 1978, fossiliferous sediments were exposed on the quarry face on the bench of 189 m. They completely filled a small cave with a height of about 2 m and a width of about 1.5 m (Fig. 6). In January and February 1978, the author excavated these sediments in collaboration with T. HAIKAWA and A. SUGIMURA, palaeontologists of the Akiyoshi-dai Museum of Natural History. The excavation revealed the following stratigraphic sequence of the sediments (described in descending order; see Fig. 6):

- Layer 1: Dark reddish brown mud which rarely contains small breccia of volcanic ash with diameters of 2 to 5 mm.
- Layer 2: Brown muddy gravel which is composed mainly of round to subround pebbles.
- Layer 3a: Reddish brown mud. A breccia of volcanic ash with a diameter of about 10 cm was observed in the western part. This layer grades eastwards into Layer 3b.
- Layer 3b: Sandy mud which rarely contains round pebbles of chert.
- Layer 4a: Yellow muddy breccia which contains limestone breccia and breccia of volcanic ash.
- Layer 4b: Reddish brown muddy breccia which contains not only breccia of limestone and travertine

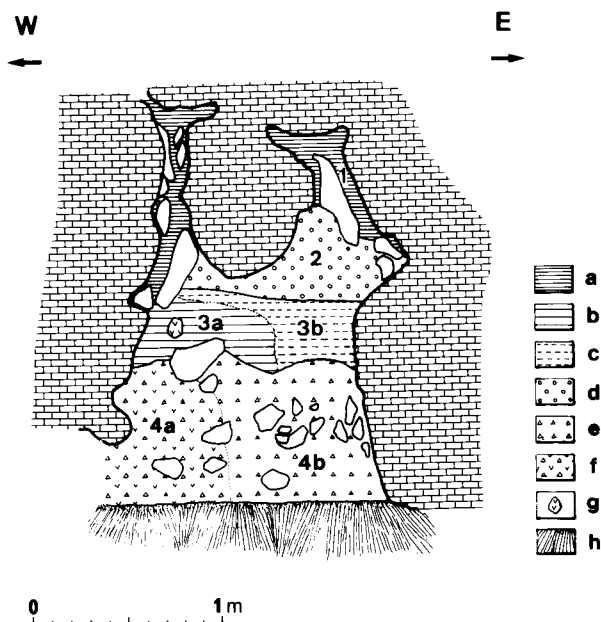


Fig. 6. Sketch showing the fossiliferous sediments of Locality 1 of Ube Kosan Quarry (drawn on 31 January, 1978).

a, dark reddish brown mud; b, reddish brown mud; c, sandy mud; d, muddy gravel (round or subround gravel); e, muddy breccia; f, muddy breccia with breccia of volcanic ash; g, breccia of volcanic ash; h, talus; 1, 2, 3a, 3b, 4a, 4b, number of layer.

but also round pebbles of chert and other kinds of rocks.

The volcanic ash contained in Layers 1, 3a and 4a as breccia is yellowish white to light yellow in colour and nearly as soft as other sediments in this cave. It is also fine grained and highly vitric. The heavy mineral composition and property of volcanic glass indicate that this ash is different from the Akiyoshi Volcanic Ash Layer which is equivalent to the pyroclastic flow called the Aso-4 in Kyushu (K. TAKEMURA, pers. comm.). It is inferred that this ash was originally deposited near this cave before the deposition of Layer 4a, and then eroded to be breccia and flowed into the cave with other sediments.

Layers 2, 3b and 4b contain round gravel. This indicates that these layers were deposited under fluvial environments. Although such gravel was never found in the sediments of Localities 3 and 4, SHIKAMA and OKAFUJI (1958) recorded the cave sediments with round gravel in other sites of this quarry which were subsequently referred to the "Middle Isa Bed" by the same authors (1963). According to their observations, these sediments were covered by brown brecciated clay which yielded *Palaeoloxodon naumanni* (described as *P. aomoriensis* in their papers), while they were underlain by hard brown clay which yielded *Stegodon orientalis*. The similarity in lithofacies possibly indicates that Layers 2, 3b and 4b are correlative with the "Middle Isa Bed."

The sediments of Layer 1 are brown mud which is similar to less brecciated part of Layers 1 to 4 of Locality 3 of the same quarry. The faunal compositions of both layers are also similar. Therefore these layers are correlative with each other.

The geological age of the sediments of Locality 1 can be estimated as the Middle Pleistocene from the correlation with those of Locality 3 which are dated by the U-series method. This age estimation is supported by the result of fluorine test and the faunal characters (especially the comparison with the proboscidean biostratigraphy established in other areas).

Locality 3 —

In 1978, fossiliferous cave sediments were found only 40 m east of Locality 1. This site was named Locality 3, and was excavated by the author in collaboration with T. HAIKAWA and A. SUGIMURA on 15 to 20 June of the same year. The excavation revealed the stratigraphic sequence of the sediments in detail. Moreover a large amount of the sediments were sampled in accordance with this sequence for the palaeontological and sedimentological analyses.

The sediments of this locality were exposed on the same quarry face as that of Locality 1 (namely that on the bench of 189 m). They completely filled two neighbouring caves (Fig. 7). Of these, the eastern cave is composed mainly of an irregular-shaped main part and isolated small pocket. A vertical column of cave limestone (flow stone, stalagmite or stalactite) is observed on the limestone bedrock above the upper border of the cave. The main part is filled mainly with mud with breccia and muddy breccia. Unfortunately, it was too dangerous to approach the eastern area of this part (A in Fig. 7), because the cave sediments and limestone bedrock there were quite easy to collapse. Therefore the sediments of this area could not be observed in detail nor sampled. However the rough observation indicates that these sediments are brown brecciated mud or muddy breccia which are continuous to Layers 4 and 6 as shown

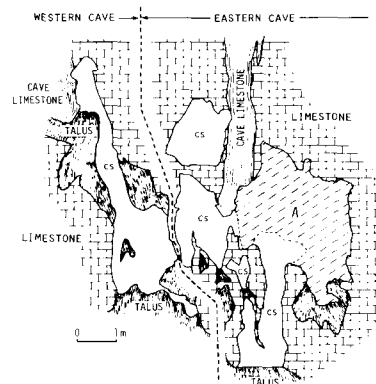


Fig. 7. Simplified diagram of Locality 3 of Ube Kosan Quarry showing the boundary between the eastern and western caves. cs, fossiliferous cave sediments; A, the cave sediments of this area could be neither observed in detail nor sampled, because it was too dangerous to approach.

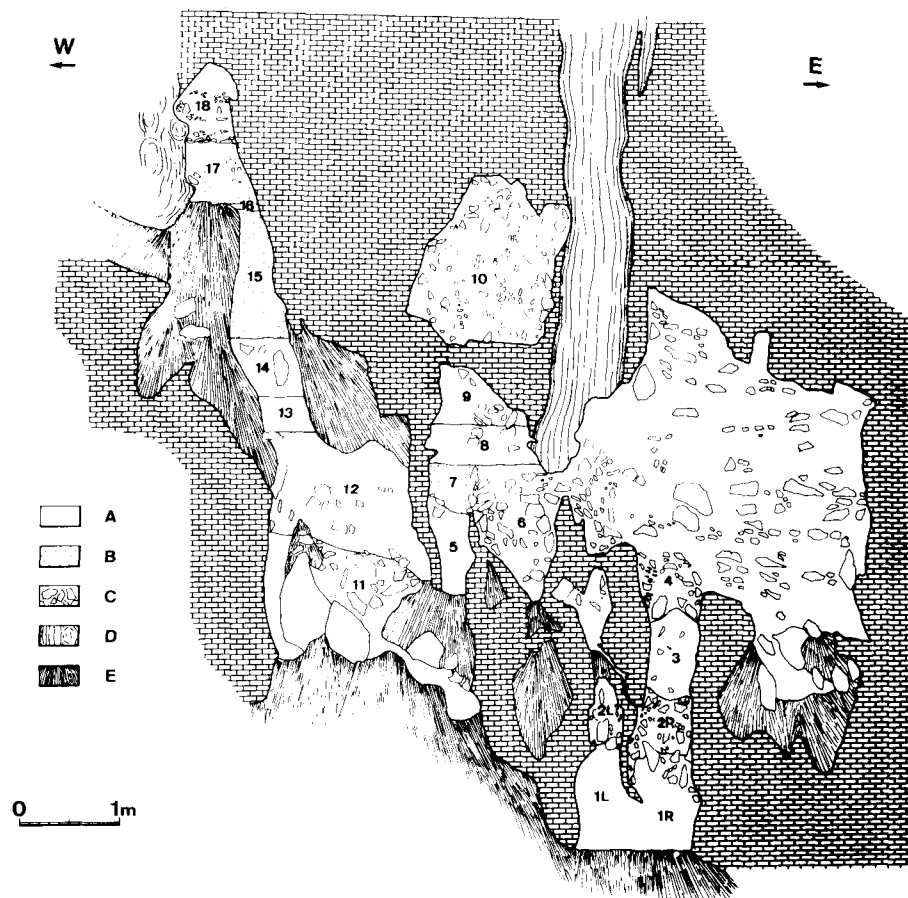


Fig. 8. Detailed sketch showing the fossiliferous sediments of Locality 3 of Ube Kosan Quarry (drawn on 15–20 June, 1978).

A, mud; B, sandy mud; C, breccia; D, cave limestone (flow stone, stalagmite or stalactite) attached on bedrock (Palaeozoic limestone); E, talus; 1–18, number of layer.

in Fig. 8 and show a strong resemblance to the sediments of Layers 4 and 6 as well as 8, 9 and 10. The isolated pocket is filled with muddy breccia (Layer 10) which is similar to the sediments of Layers 4 and 6. It is inferred that this pocket formed an ascending branch of the main part before the destruction of the cave by limestone working. Therefore Layer 10 was possibly underlain by Layer 9.

The detailed descriptions of each layer of the eastern cave are given below, which include the gravel composition deduced from the examination of more than 175 breccia with pebble- and cobble-size (see Fig. 9):

- Layer 1: Brown mud with breccia. The breccia is composed mainly of limestone and cave limestone. This layer is subdivided into the left part (1L in Fig. 8) and right part (1R) by a thin vertical wall. The sediments of both parts are continuous and nearly identical with each other, but the composition of breccia is somewhat different. Namely limestone breccia is more abundantly contained in the left part (67.4%) than in the right part (47.3%), while breccia of cave limestone is less abundant in the former (30.7%) than in the latter (47.3%). The average composition of both parts is given in Fig. 9, which is nearly the same as that of Layer 2.
- Layer 2: Brown muddy breccia. This layer is also subdivided into the left part (2L in Fig. 8) and right part (2R). The lithofacies of both parts are quite similar to each other, but the diameter of breccia is somewhat larger in the right part (20 cm in maximum) than in the left part. Moreover the gravel composition is somewhat different between these parts. Namely the ratio of cave limestone (55.9%) exceeds that of limestone (43.2%) in the left part, while the former is lower than the latter in the right part (30.9% and 66.4% respectively).
- Layer 3: Brown mud with breccia. The breccia attains to 15 cm in maximum diameter. The gravel composition is nearly identical with the average of Layer 1 as well as that of Layer 2.
- Layer 4: Brown muddy breccia to brecciated mud. The maximum diameter of the breccia attains to 40 cm. The gravel composition is characterized by the predominance of limestone (75.8%) and relative scarcity of cave limestone (22.4%).
- Layer 5: Reddish brown muddy breccia. The breccia is pebble-sized and composed mainly of limestone (56.5%) and cave limestone (35.2%), but breccia of chert is rarely contained (0.8%). The breccia of cave limestone is mostly well-crystallized.
- Layer 6: Dark brown muddy breccia. The breccia attains to about 15 cm in maximum diameter, and is composed mainly of limestone (56.1%) and cave limestone (39.0%). The breccia of cave limestone is mostly well-crystallized as in Layer 5. This layer is continuous to the upper part of Layer 4, and lithologically similar to Layer 11 of the western cave.
- Layer 7: Reddish brown sandy mud with breccia of cave limestone.
- Layer 8: Brown sticky mud with breccia. The gravel composition resembles that of Layer 6.
- Layer 9: Brown mud with breccia. The maximum diameter of breccia attains to 10 cm. The gravel composition is similar to that of Layer 6, but the present layer sometimes contains orange breccia of flow stone.
- Layer 10: Dark brown muddy breccia. The lithofacies is similar to that of Layer 6 as well as that of Layer 11 in the western cave. The gravel composition is nearly identical with that of Layer 6.

The western cave shows fissure-like appearance, and is separated from the eastern cave by a thin vertical wall (Fig. 7). The upper part of the western wall of the cave is covered by flowstone-like cave limestone. This cave is filled with muddy breccia (Layer 11), mud with breccia (Layers 12, 13, 14, 16 and 18) and sandy mud (Layers 15 and 17). Although the sediments of Layer 11 are similar to those of Layers 4, 6 and 10 of the eastern cave, the lithofacies of other layers of this cave are considerably different from those of any layer of the eastern cave. Each layer of this cave is closely described as follows (including the gravel composition obtained by the same method as in the eastern cave; see Fig. 9):

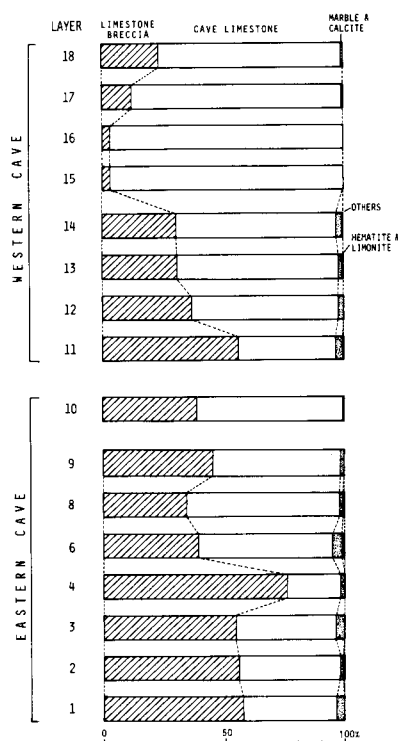


Fig. 9. Gravel composition in each layer of Locality 3 of Ube Kosan Quarry. More than 175 breccias with pebble- and cobble-size are examined in each layer.

- Layer 11: Dark brown muddy breccia. The breccia is composed mainly of limestone (56.0%) and cave limestone (40.4%).
- Layer 12: Dark brown mud with breccia. The breccia is usually pebble-sized, but sometimes cobble-sized. As regards the gravel composition, the ratio of cave limestone (61.0%) exceeds that of limestone (36.5%).
- Layer 13: Reddish brown mud with pebble-sized breccia. The gravel composition is similar to that of Layer 12.
- Layer 14: Brown sticky mud with breccia. The gravel composition is nearly equal to that of Layer 13. In this layer, however, breccia of sandstone and shale is rarely contained (0.2% and 0.4% respectively).
- Layer 15: Red sandy mud with pebble-sized breccia. As regards the gravel composition, cave limestone predominates (96.2%), while limestone is rare (3.5%). In the breccia of cave limestone, travertine with tabular shape is frequently found, which is also abundantly contained in Layers 16 and 17.
- Layer 16: Dark brown mud with breccia. The composition of breccia is identical with that of Layer 15.
- Layer 17: Reddish brown sandy mud with pebble-sized breccia. The ratio of the breccia of cave limestone (87.0%) is somewhat lower than those in Layers 15 and 16, while that of limestone (12.6%) is higher than in these layers.
- Layer 18: Dark brown sticky mud with breccia. The breccia is composed mainly of cave limestone (76.1%) and limestone (23.4%) which are sometimes weathered. The breccia of cave limestone is sometimes orange in colour. Bones of large mammals and charcoal grains (ca. 5 mm in diameter) are abundantly contained. In the lower part of this layer, tabular breccia of cave

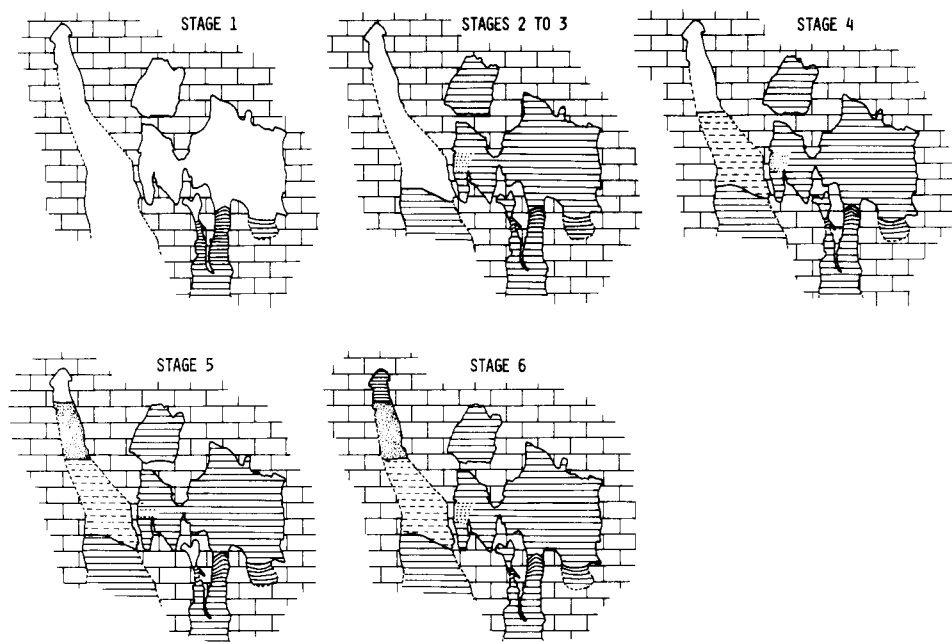


Fig. 10. Schematic diagram showing the depositional history of the caves of Locality 3 of Ube Kosan Quarry. For detailed explanation see text.

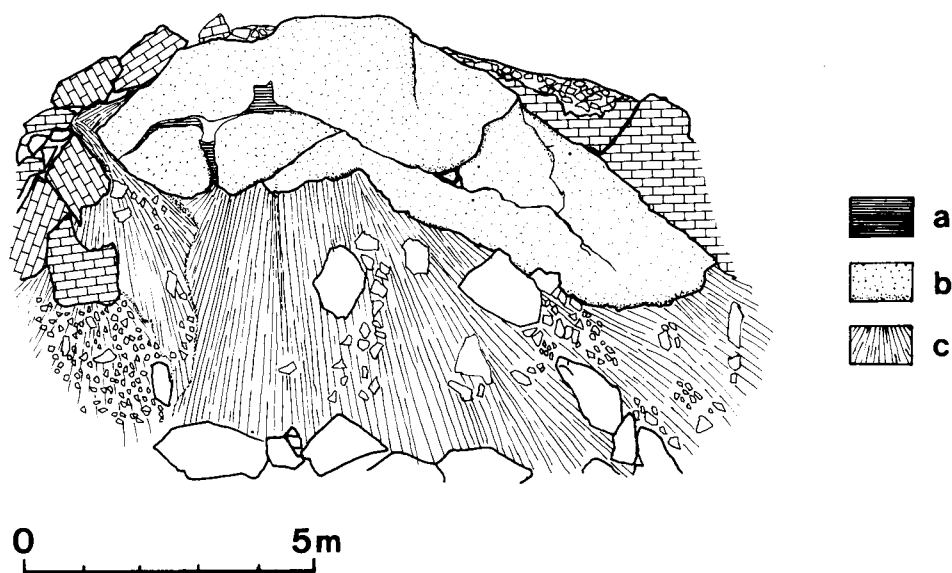


Fig. 11. Sketch of the cliff at Locality 4 of Ube Kosan Quarry (drawn on 23 August, 1978).
a, fossiliferous brown mud; b, wall of destroyed cave; c, talus.

limestone and long bones of large mammals are arranged along the lower boundary of the layer. On the other hand, only 16 cm above this boundary, a lamina of orange mud is intercalated, which is 4 cm. in maximum thickness and thins off eastward.

The lithological similarity of Layer 11 of the western cave to the upper layers of the eastern cave (especially Layers 6 and 10) indicates that these layers were deposited under the same sedimentary environment, and are roughly correlative with each other. When the stratigraphic sequences of both caves are taken into consideration, it is most probable that Layer 10 of the eastern cave is overlain by Layer 11 of the western cave, but the deposition of the latter layer is almost synchronous with, or slightly later than that of the upper layers of the eastern cave. Based on such correlation, the following depositional history of these caves is deduced (Fig. 10):

- Stage 1: The deposition began in the eastern cave. The sediment was transported from the other places of a presumptive large cave which included the eastern and western caves as its parts, as well as from the outside of the cave. Layers 1 to 3 were deposited in this stage.
- Stage 2: The eastern cave was completely filled with the sediment, while the western cave was still vacant. The sedimentary environment remained unchanged from the stage 1. This stage is represented by Layers 4 to 10.
- Stage 3: The sediment first flowed into the western cave to form Layer 11. The similar environment to the stage 2 was persistent.
- Stage 4: The sedimentary environment was gradually changed to form the sediment somewhat different from those in the previous stages. Layers 12 to 14 were deposited in this stage.
- Stage 5: The sedimentary environment in this stage was considerably different from those in other stages. Namely, the inflow of the sediment from the outside of the cave was almost stopped, so that the sediment of cave-origin was predominantly deposited. This stage is represented by Layers 15 to 17.
- Stage 6: The sedimentary environment was again changed. The inflow of the sediment from the outside of the cave increased. Layer 18 was deposited in this stage.

In order to estimate the geological age of the sediments of this locality, fossil bones and travertine collected from several layers were dated by the U-series, amino-acid and fluorine dating methods. A fragment of travertine from Layer 3 gives a date of about 0.19 m.y. by the first method, while bone fragments from Layer 17 is dated as about 0.15 m.y. by the second method (KOMURA, HAYASHI and MATSU'URA; pers. comm.). Therefore all the layers of this locality are considered to be late Middle Pleistocene in age. Such age estimation is consistent with the results of fluorine analysis as well as the faunal characters of each layer.

Locality 4 —

Because the author and T. HAIKAWA were informed by an employee of the company that fossil bones had been found in cave sediments exposed on the bench of 140 m near the cement plant of the company, they visited there by the guidance of the employee on 23 August, 1978 (Loc. 4 in Fig. 5). Unfortunately the fossiliferous cave had been almost destroyed, and they could find only a cave wall remained on a quarry face (Fig. 11). This wall shows solutional features and is partly covered by cave limestone. On this wall, small pockets were formed along cracks. They were filled with brown mud which exclusively yielded micro-mammalian fossils. These fossils are badly preserved, because they suffered strong chemical solution. The fossiliferous sediments are estimated to be Middle Pleistocene in age only from the faunal characters.

B. Late Pleistocene localities

1. Aisawa (Aizawa) Quarry

The occurrence of fossil bones of *Meles* from this quarry was first recorded by SHIKAMA (1933). The stratigraphic sequence of the fossil-bearing sediments was subsequently provided by the same author (1937b, 1949). In addition to these works, KOWALSKI and HASEGAWA (1976) described five specimens of rodents belonging to three taxa from this quarry.

On 3 May, 1981, the present author visited this locality with the guidance of T. NOMURA who had found a fossiliferous fissure there a few years before. Although this quarry was called Yoshizawa Quarry, Aisawa in SHIKAMA's papers, it was subsequently renamed Aisawa Quarry of Nittetsu Mining Company owing to the change of its owner. The fossiliferous fissure was exposed on a high quarry face, and filled with brown brecciated mud (Fig. 13). Judging from the figures provided by SHIKAMA (1937b; Figs. 17 and 18 of Pl. 6), the present fissure is probably the same one as shown in these figures, although the features are somewhat different from each other.

At the time of the visit of the author, it was too dangerous to approach this fissure, but many fossil bones were found in talus sediments fallen down from the fissure. These sediments

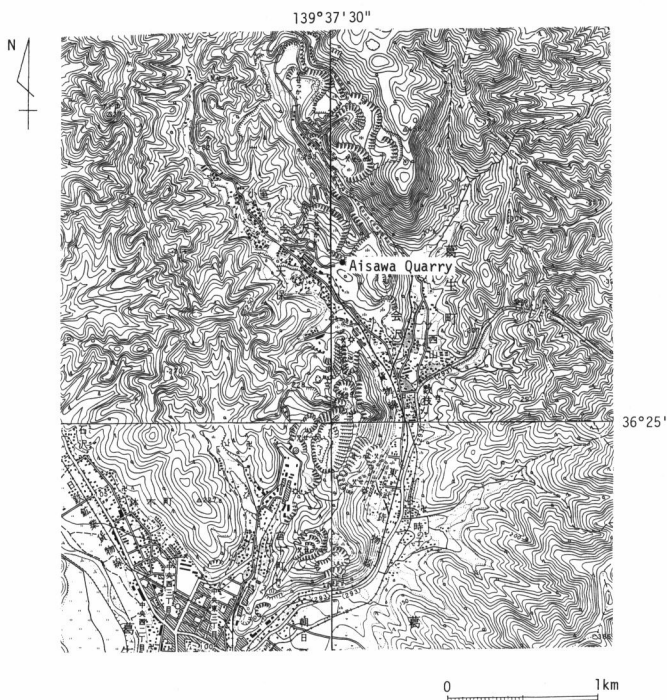


Fig. 12. Index map showing the location of Aisawa Quarry. The scale 1:25,000 map sheets "Shimotsuke-ogaki," "Senba," "Tochigi" and "Tanuma" published by the Geographical Survey Institute are used.

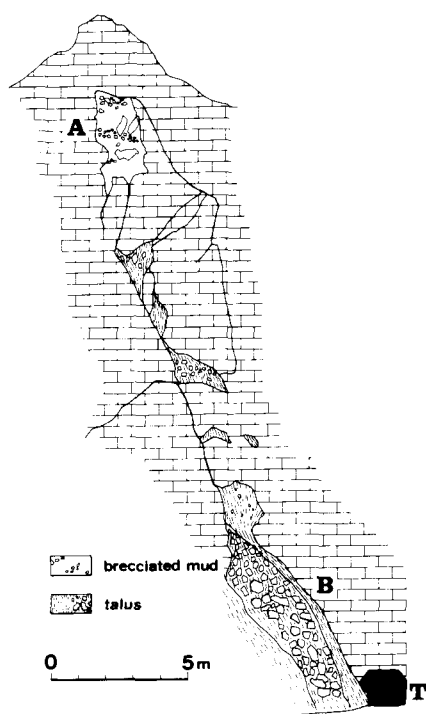


Fig. 13. Fossiliferous fissure sediments at Aisawa Quarry of Nittetsu Mining Company. A, fissure filled with original sediments (brecciated mud). From A to B, these sediments are fallen down along the surface of this cliff to form talus; B, talus sediments where the mammalian fossils examined here were collected; T, tunnel for mining. Originally drawn on 3 May, 1981.

were sampled for washing and screening. As the results of the screening, micro-mammalian fossils were obtained more variously and abundantly than those reported in the previous works. A block of the fossiliferous sediments with roots of a tree was found in the talus. This block contained volcanic ash which was assignable to the Kanuma Pumice Bed. This bed is a remarkable horizon marker in this area, which is dated as $32,000 \pm 4000$ or $31,000 \pm 8000$ yr. B.P. by the fission-track method (SUZUKI, 1976). It is assumed that the land surface above this quarry face is covered by this pumice bed which is underlain by the fossiliferous brecciated mud as observed in other localities of this area by SHIKAMA (1937b, 1949).

On the basis of these observations, the present fossiliferous sediments are undoubtedly referred to the Upper Kuzuü Formation of SHIKAMA (1949) which is considered to be Late Pleistocene in age from the stratigraphic relationship with the Kanuma Pumice Bed and its faunal characteristics.

2. Nojiri-ko Formation

The Nojiri-ko Formation is considered to be one of the most important strata in the Japanese Late Pleistocene, because it yields not only numerous fossils (vertebrates, insects, molluscs, plants etc.) but also human artifacts. This formation occurs below the bottom of Lake Nojiri (Nojiri-ko), and is composed of lacustrine sediments with intercalations of many layers of pyroclastic sediments. The stratigraphic sequence of the formation is well-

investigated by GEOLOGY RESEARCH GROUP FOR NOJIRI-KO EXCAVATION (1975, 1977, 1980, 1984). This formation is divided into three members such as the Lower, Middle and Upper Members. Each member is also subdivided into three sections (I, II and III in ascending order). The range of ^{14}C dates obtained from each member is given as follows (after Figs. 1–3 of GEOLOGY RESEARCH GROUP FOR NOJIRI-KO EXCAVATION, 1984):

Upper Member $16,290 \pm 720$ to $25,600 \pm 1500$ yr. B.P.

Middle Member $22,940 \pm 990$ to $27,680 \pm 1950$ yr. B.P.

Lower Member..... $25,350 \pm 1100$ to $41,860 \pm 3220$ yr. B.P.

Mammalian fossils occur from the Section III of the Lower Member to the Section I of the Upper Member (THE EDITORIAL COMMITTEE OF MONOGRAPH NO. 27 OF THE ASSOCIATION FOR THE GEOLOGICAL COLLABORATION IN JAPAN, 1984).

3. Sugi-ana Cave

Sugi-ana Cave is a deep inclined cave which opens on a ridge about 350m north-northwest of Higashi-akuda (Fig. 14). The speleological survey of this cave was first carried out by KAJITA (1970) who provided its detailed plan and section. Although he did not record the occurrence of fossil bones, K. KAJIURA and students of Gujo Highschool subsequently discovered numerous mammalian fossils in this cave. These fossils were preliminarily studied by KAWAMURA and KAJIURA (1980).

From a small entrance with the altitude of 580 m, a narrow tunnel extends north-northeastward, which dips 60° in average. The fossil sites are situated at the middle of this tunnel (Fig. 15). Between depths of 60 m and 70 m, the tunnel remarkably broadens to be a hall. From this hall, another narrow horizontal tunnel extends southward in a length of about

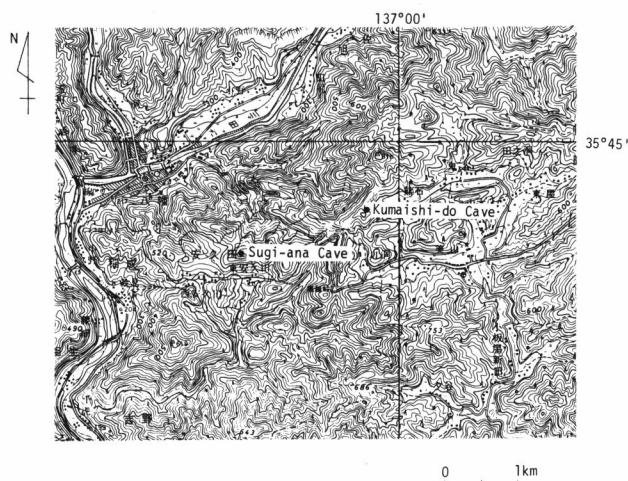


Fig. 14. Index map showing the locations of Kumaishi-do Cave and Sugi-ana Cave. The scale 1:50,000 map sheets "Hachiman" and "Gero" published by the Geographical Survey Institute are used.

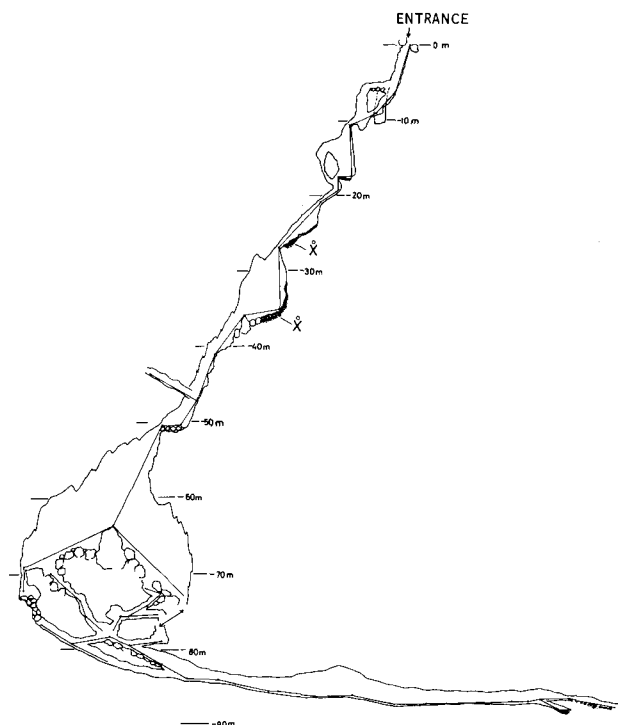


Fig. 15. Cross-section of Sugi-ana Cave showing the locations of the fossil sites (modified from KAJITA, 1970). X fossil site.

30 m, and then turns westward. This tunnel is traceable about 30 m ahead from this turning point.

In the fossil sites, fossiliferous muddy sediments are observed on the cave floor. Because unfossilized fresh bones are sometimes found in these sediments, it is inferred that recent bones of mammals flowed down with soil from the entrance and mixed with the Pleistocene sediments. Moreover these Pleistocene sediments were possibly transported from another place in this cave and also redeposited in the present sites. Unfortunately the place where these sediments were originally deposited has been hitherto unknown.

The exact age of the Pleistocene sediments is estimated by the fluorine and amino-acid dating methods (MATSU'URA, pers. comm.). Although the fossil bones from these sediments exhibit wide ranges of variation in fluorine content and in state of fossilization, the sediments can be approximately dated as the early Late Pleistocene. The chronological problems and correlation with other fossil localities will be discussed in Chapter VI.

4. Kumaishi-do Cave

Kumaishi-do Cave opens on the southern slope of Mt. Chigosan (818.7 m in elevation)

about 1.8 km east-northeast of Sugi-ana Cave (Fig. 14). The elevation of its entrance is estimated to be about 640 m above sea level.

The occurrence of the Pleistocene mammals from this cave was first reported by CHIJU *et al.* (1966). Soon after the publication of this report, HIURA (1967) and HASEGAWA (1968) pointed out the significance of these mammals, especially that of *Alces* which was an immigrant from taiga forests. In 1969, OKUMURA provided a preliminary faunal list of these mammals and compared it with those of other fossil localities. In 1971, KAJITA *et al.* published the result of the speleological exploration of this cave. Since 1975, the excavations of the fossiliferous sediments and palaeontological studies of the mammals have been actively carried out by the "Miyama Research Group" headed by K. OKUMURA in which the present author has joined as a member. The results of these works were succeedingly published by the members of the group (KAWAMURA and ISHIDA, 1976; KAWAMURA, 1977a; OKUMURA *et al.*, 1978, 1982; ISHIDA and OKUMURA, 1982).

According to KAJITA *et al.* (1971), this cave is made up of the combination of two elements such as narrow vertical pit and relatively broad horizontal tunnel (see the figure in p. 385 of their paper). The former element is predominant in the upper part of the cave, while the latter is well-developed in the lower part. Because the fossiliferous sites are restricted to the upper part, the description of this part is exclusively given below.

From the entrance, a vertical pit leads us to the first hall (H_1) which extends in a east-west direction (Fig. 16). Huge limestone blocks are piled up on its floor. HASEGAWA (1968) reported the Holocene mammalian remains from black earth at the eastern end of this hall just below the entrance. This earth is, however, different in lithofacies and geological age from the fossiliferous sediments described below. Two deep pits open at the eastern and western ends of this hall. They become confluent about 10 m below the hall. A narrow passage (F_1) steeply

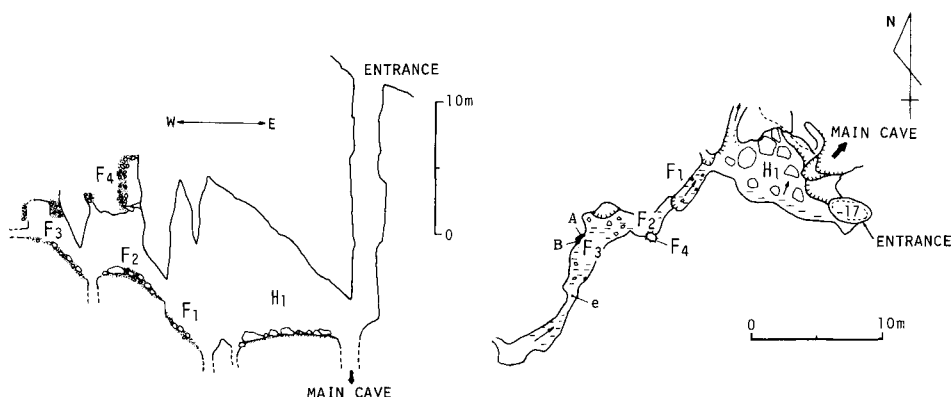


Fig. 16. Section and plan of Kumaishi-do Cave showing the positions of the fossil sites (H_1 , F_1 - F_4). The area near the entrance is exclusively shown. The section (left-hand figure) is redrawn from OKUMURA *et al.* (1982), while the plan (right-hand figure) is simplified from KAJITA *et al.* (1971). A, B, two faces of the outcrop of the fissure sediments at F_3 (see Fig. 19). e, entrance of the tunnel at the southwestern end of F_3 .

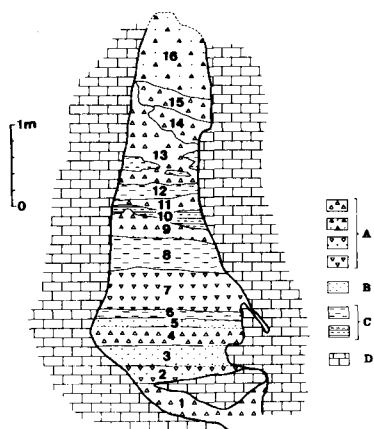


Fig. 17. Explanatory sketch showing the fossiliferous fissure at F₄ of Kumaishi-do Cave. A, muddy or sandy breccia; B, sand with breccia; C, mud with breccia; D, limestone. For detailed explanation of each layer see text. This figure was drawn on 18 August, 1978.

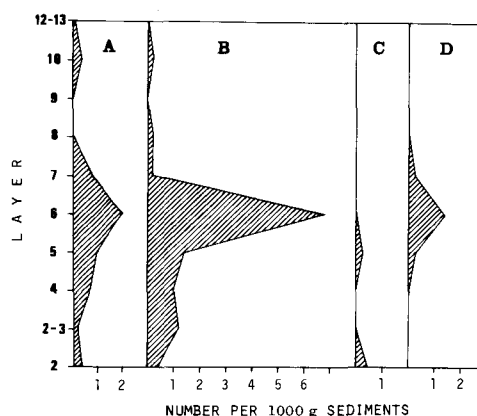


Fig. 18. Relative abundance of the micro-mammalian remains in each layer of F₄ of Kumaishi-do Cave. Number of specimens per 1,000 g sediments is shown.

A, incisors of rodents; B, molars of rodents; C, molars of lagomorphs; D, mandibles of insectivores and chiropterans.

ascends south-westward from the western end of the hall. Reddish brown mud is deposited on its floor. This mud contains mammalian fossils, and flows down from an upper small chamber (F₂). On the floor of F₂, the same fossiliferous mud is deposited.

A small pit opens on the upper part of the southern wall of F₂. It extends upward. This pit is called F₄, and terminates about 5m above its entrance. Stratified fissure sediments are observed on its western wall (Fig. 17). These sediments are reddish brown to greyish brown in colour, and composed mainly of muddy or sandy breccia and mud with breccia. Limestone and chert breccia is predominantly found in the sediments, because these rocks comprise the bedrock of this cave. The sediments are divided into 16 layers which are closely described below in descending order.

Layer 16: Muddy breccia. The breccia ranges from 3 to 4 cm in diameter.

Layer 15: Sandy breccia. The breccia ranges from 2 to 3 cm in diameter.

Layer 14: Sandy breccia which intercalates thin layers of muddy breccia.

Layer 13: Sandy breccia with lenses of reddish brown brecciated mud.

Layer 12: Mud with breccia. The breccia is rather scarcely contained, and is generally 5 cm in diameter.

Layer 11: Sandy breccia. The breccia ranges from 1 to 20 cm in diameter.

Layer 10: Mud with breccia. The breccia ranges from 3 to 5 cm in diameter.

Layer 9: Weakly-laminated sandy breccia. This layer is similar to Layer 11.

Layer 8: Mud with breccia of 7 to 8 cm in diameter. The breccia is scarcely contained.

Layer 7: Sandy breccia. Breccia with diameter around 3 cm is predominantly contained, but larger breccia (10 to 15 cm in diameter) is scarce.

Layer 6: Mud with breccia of 4 to 5 cm in diameter. This layer is relatively rich in breccia, and is

bordered from Layer 5 by a thin limonite bed.

Layer 5: Muddy sand with breccia of 1 to 2 cm in diameter.

Layer 4: Sandy breccia. The breccia is pebble-sized.

Layer 3: Sand. A thin limonite bed is intercalated between this layer and Layer 2.

Layer 2: Sandy breccia. The breccia attains to 20 cm in maximum diameter. This layer is bordered from Layer 1 by a thin limonite bed.

Layer 1: Sandy breccia. The breccia attains to 20 cm in maximum diameter.

The mammalian fossils are obtained from all the layers, but the mode of occurrence of each taxon varies from layer to layer. Namely, the fossils of *Palaeoloxodon naumanni* and *Sinomegaceros yabei* are found in Layers 1 to 5, while those of *Alces alces* are almost restricted to Layer 1. The remains of *Cervus praenipponicus* are concentrated to Layers 9 to 11. As regards micro-mammals, Layer 6 contains them in highest frequency (Fig. 18).

The sediments of F₄ fall down to the eastern part of F₂, and then flow down to F₁ (Fig. 16). Therefore the sediments of F₁ and F₂ are fundamentally identical with those of F₄.

A vertical pit opens at the western end of the floor of F₂, where F₂ is connected to an inclined passage (F₃). This passage suddenly tapers south-westward to be a tunnel with a height of only 1.6 m or less. This tunnel is traceable about 9 m ahead. On the western wall

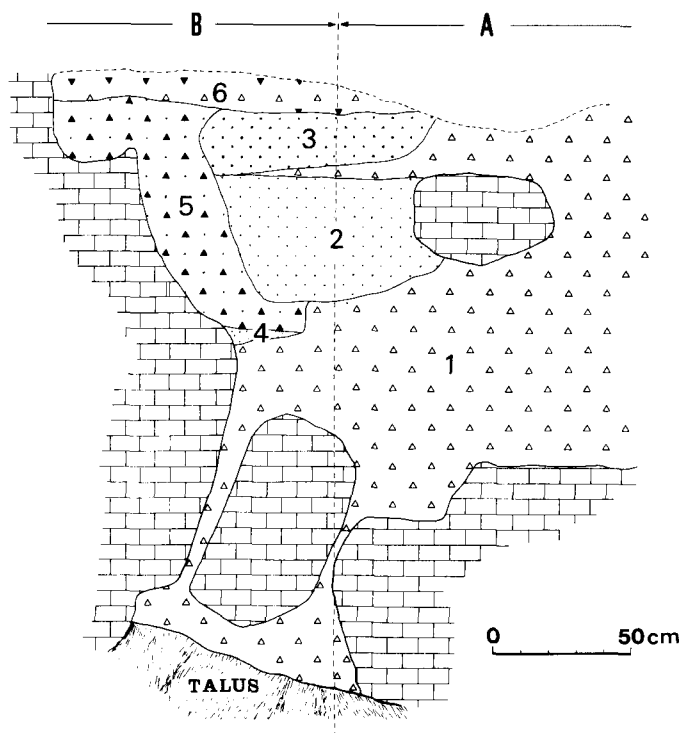


Fig. 19. Fossiliferous sediments of F₃ of Kumaishi-do Cave. The sediments are exposed on two right-angled faces (A and B; see Fig. 16). These faces are unfolded into a single plane in this figure. 1, 5, 6, muddy breccia; 2, 3, 4, muddy sand. For detailed explanation of each layer see text. This figure was drawn on 30 April, 1978.

of F₃, fossiliferous fissure sediments are exposed (Fig. 19). These sediments are brown in colour, and can be divided into the following six layers:

- Layer 6: Muddy breccia. The matrix is more sandy than that of Layer 5.
- Layer 5: Muddy breccia. The breccia is pebble-sized.
- Layer 4: Thin bed of sand.
- Layer 3: Muddy coarse sand with pebble-sized breccia.
- Layer 2: Muddy coarse sand which contains breccia of 5 cm in diameter.
- Layer 1: Muddy breccia. The breccia attains to 20 cm in maximum diameter.

As shown in Fig. 19, these layers are irregularly deposited and laterally changed to each other. Moreover the boundaries between them are rather obscure. The fossils are obtained from all the layers. They are mostly assignable to micro-mammals.

Another small fissure is observed above the entrance of the tunnel at the southwestern end of F₃ (e in Fig. 16). This fissure is 0.2 to 0.6 m in width and at least 1.8 m in height. It is filled with brown mud and breccia. Such sediments as well as those exposed on the western wall fall down to the floor of F₃, and flow down to the pit which opens at the western end of F₂.

Fossil bones collected from Layers 4 and 5 of F₄ are dated as $16,720 \pm 880$ yr. B.P. by the ¹⁴C dating method (OKUMURA *et al.* 1982). On the other hand, the fluorine analysis indicates that the sediments of F₃ are somewhat older than those of F₄ (MATSU'URA, pers. comm.), but both of them are considered to be Late Pleistocene in age. Such age estimation is well coincident with the faunal characters of these sediments.

5. Yage Quarry (partly including the Middle Pleistocene sediments)

Yage is a small village about 1 km northeast of Inoya, a main town of Inasa-cho (Fig. 20). A small limestone lens intercalated in other sedimentary rocks (chert, clayslate etc.) crops out around this village, and was mined by Kawai Sekkai Company in so-called Yage Quarry

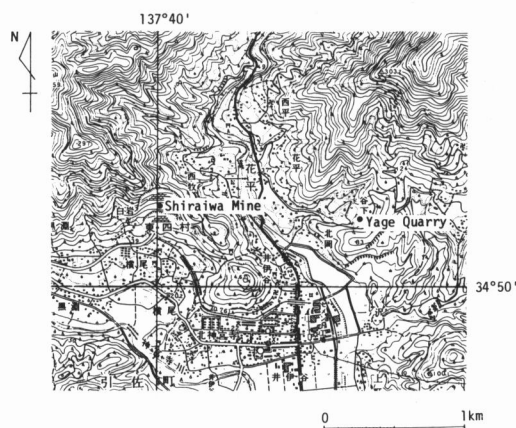


Fig. 20. Index map showing the locations of Yage Quarry and Shiraiwa Mine. The scale 1:25,000 map sheets "Idaira" and "Kiga" published by the Geographical Survey Institute are used. Shiraiwa Mine is another important fossil locality which yielded abundant micro-mammalian remains (see p. 35).

(=Kawai Limestone Quarry). Since the 1950's, the Quaternary vertebrate fossils have been occasionally found in fissure sediments exposed on quarry faces of this quarry. The first report on these fossils appeared in 1958, which dealt with mandibles of young elephant (TAKAI *et al.*, 1958). In 1965, UYENO noticed the occurrence of an exotic form of cyprinid fish from this quarry. A preliminary faunal list of the fossils was first provided by ISOMI and INOUE (1972), where 9 forms of mammals and 3 forms of other vertebrates were listed. In 1978, TOMIDA gave a more complete list and briefly described many fossils collected by himself and his co-operators. He also attempted to give an explanation of the stratigraphy of the fissure sediments. In addition to these works, students of Hamamatsu-kita High School and many amateur palaeontologists collected a number of vertebrate fossils from this quarry. Unfortunately their collections have scarcely appeared in scientific literatures.

Since 1976, the author has occasionally visited this quarry to collect the fossils and to observe the stratigraphic sequence of the fissure sediments. He also investigated the Hamamatsu Formation distributed in the neighbouring area south of this quarry in 1977. This formation is composed mainly of fluvio-lacustrine and marine sediments, and is considered to be Middle Pleistocene in age. The purpose of the investigation was to correlate it with the fissure sediments. Moreover the author could examine Y. MATSUHASHI's private collection which included many mammalian fossils collected from this quarry before 1976. MATSUHASHI also gave the author important information on the sediments which yielded these fossils.

In this quarry, the fossiliferous fissure sediments were exposed at six sites (Sites 1 to 6) which are shown in the plan (Fig. 21). These sites are closely described below:

Site 1 —

The fossiliferous fissure was exposed on the western slope of a hillock which was present at the position of Site 1 in Fig. 21. This hillock was completely destroyed to be a quarry floor, before the author first visited this quarry. Therefore it is not shown in Fig. 21. But fortunately, the plan of this hillock is recorded in TOMIDA (1978, Fig. 2).

As his personal communication, MATSUHASHI informed the author that the fossiliferous fissure was about 5 m in height and more than 6 m in width, and was filled with the following sediments (described in descending order):

4. brown mud with a thickness of 2.5 m or more.
3. white weathered volcanic ash with a thickness of 1.2 m.
2. bluish grey mud which contains numerous fish bones (0.5 m in thickness).
1. gravel which contains fossils of crocodile and turtle (0.5 m in thickness).

The lower part of the brown mud contains numerous fish bones which resemble those in the bluish grey mud, while the upper part is characterized by the abundant occurrence of land vertebrates. Such a clear difference suggests that a time gap is interposed between the periods of the sedimentation of both parts. The fossil evidences indicate that the lower part of the brown mud, volcanic ash, bluish grey mud and gravel were continuously deposited under estuarine or lagoonal environments when the sea level was high. These sediments are correlative with a marine or brackish silt bed of the Hamamatsu Formation exposed near this quarry, and therefore Middle Pleistocene in age. Such age estimation is supported by the

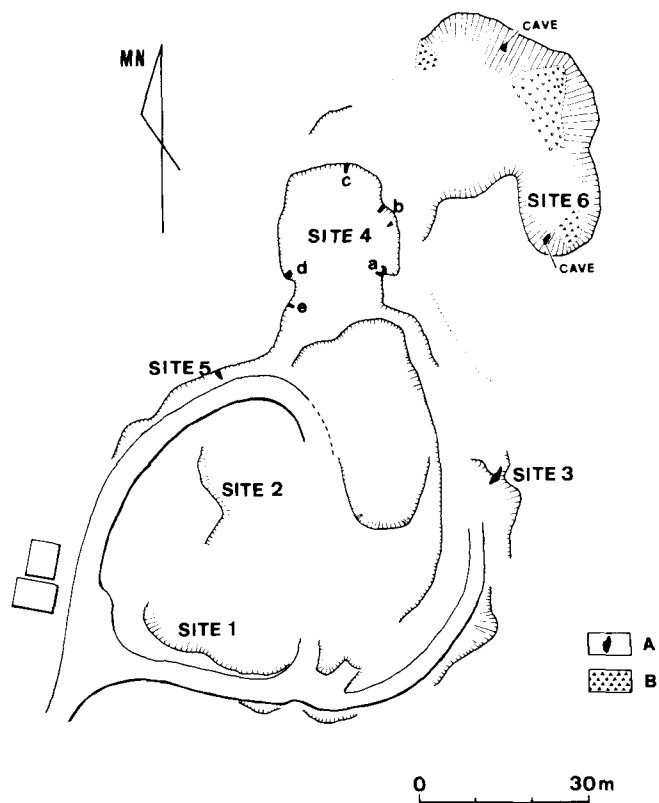


Fig. 21. Plan of Yage Quarry showing the location of each site. Original figure drawn on 18 September, 1977. A, fossiliferous fissure; B, talus.

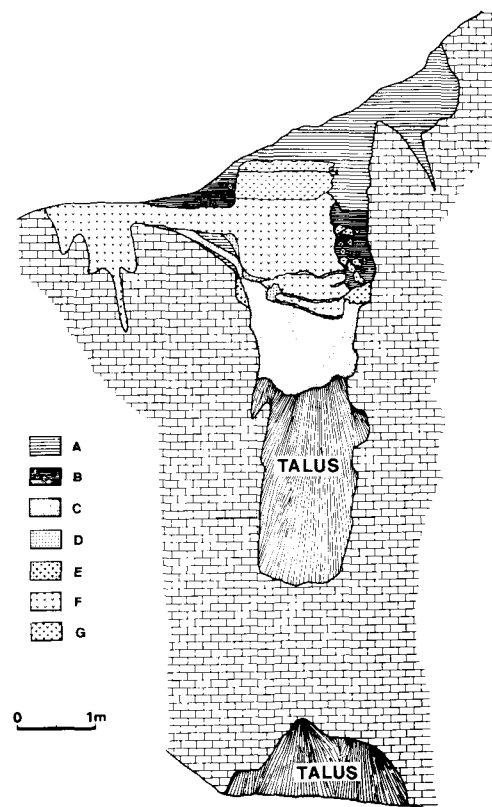


Fig. 22. Sketch showing the fissure sediments exposed at Site 3 of Yage Quarry (originally drawn by K. TAKEMURA in 1976).

A, mud; B, mud with breccia of the volcanic ash (F and G); C, muddy sand; D, coarse sand with gravel; E, gravel; F, pinkish white argillated volcanic ash; G, greyish white volcanic ash.

result of the fluorine analysis of fish bones which were collected from brown mud exposed at Site 3 (MATSU'URA, pers. comm.; see Table 17), because this mud is equivalent to the lower part of the brown mud at the present site.

On the other hand, the upper part of the brown mud is quite similar to the sediments of Sites 4 and 5 not only in lithofacies but also in faunal composition. As discussed in the subsequent section, the latter sediments are assigned to the Late Pleistocene. Therefore the upper part of the present mud is considered to be of the same age. All of the fossils examined in the present study were collected from this part by MATSUHASHI.

Site 2 —

The fossiliferous sediments of this site were also completely lost, when the author first visited this quarry. However TOMIDA (1978) recorded four fossiliferous fissures at this site which were called A, B, C and L by him. According to TOMIDA, the sediments of these fissures are composed mainly of brown clay, yellowish brown sandy clay and brown brecciated clay. Because these sediments strongly resemble those of Sites 4 and 5 in lithofacies and faunal composition, they are considered to be Late Pleistocene in age (see the descriptions of Sites 4 and 5). In the present study, the fossil specimens collected by MATSUHASHI are exclusively examined, but the exact position and horizon of their occurrence are unfortunately unknown.

Site 3 —

This site corresponds to Fissure F of TOMIDA (1978). As shown in Fig. 22, the fossiliferous fissure is exposed on the upper part of the quarry face. It is 1.5 to 3 m in width and about 3.5 m in height. The basal part of the fissure is filled with muddy sand which intercalates thin lenses of gravel and mud in its upper part. This sand yields fossil bones of crocodile as stated by TOMIDA (1978), and is overlain by a volcanic ash layer. This ash layer is divided into two parts, namely pinkish white argillated ash in the lower part and greyish white ash in the upper part. The upper surface of this layer is strongly eroded to be an irregular shape. This layer is overlain by reddish brown mud which contains numerous fish bones. The lower part of the mud abundantly contains breccia of the volcanic ash.

The stratigraphic sequence of these sediments is nearly identical with that of the sediments of Site 1. However the brown mud which yields rich mammalian fossils could not be found at Site 3 by the investigation of the present author. As mentioned in the section of Site 1, the correlation with the Hamamatsu Formation and the fluorine analysis of fish bones from the reddish brown mud indicate that all the sediments of Site 3 described above are Middle Pleistocene in age.

Mammalian remains are very rare in the sediments of this site. Teeth of bats are scarcely found only in the reddish brown mud in association with numerous fish bones.

Site 4 —

More than five fossiliferous fissures were found at this site (Fig. 21). Because the sediments of these fissures are quite similar to each other, they are correlative with each other. The fluorine analysis of fossil bones from one of these fissures suggests that the sediments of this fissure are Late Pleistocene in age (MATSU'URA, pers. comm.; see Chapter VI), and therefore those of other fissures are possibly assigned to the same age. On the other hand, the similarity

in lithofacies indicates that the sediments of this site are also correlative with those of Site 5 which are dated as the Late Pleistocene by the ^{14}C method. Such a correlation supports the above-mentioned age estimation of the present sediments.

In order to describe each fissure in detail, this site is subdivided into five sites corresponding to five major fissures (namely 4-a, 4-b ... 4-e; see Fig. 21). The description of each site is given below.

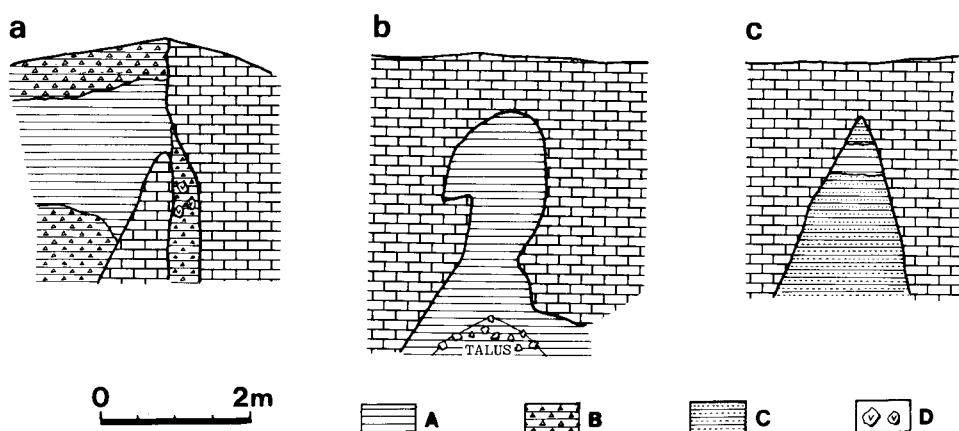


Fig. 23. Schematic sketch of the fissure sediments observed at Sites 4-a, 4-b and 4-c of Yage Quarry. a, Site 4-a; b, Site 4-b; c, Site 4-c; A, mud; B, mud with breccia or muddy gravel; C, muddy sand; D, breccia of the volcanic ash exposed at Site 3. This figure was drawn in 1977.

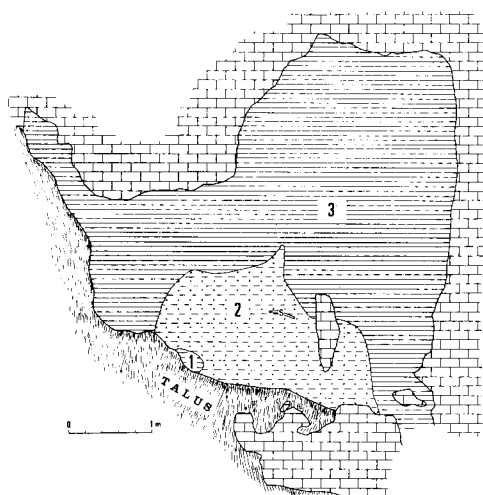


Fig. 24. Sketch of the fissure or cave sediments exposed at Site 4-d of Yage Quarry. 1, 3, mud; 2, muddy gravel; s, thin lens of sand. This figure was drawn on 18 August, 1982.

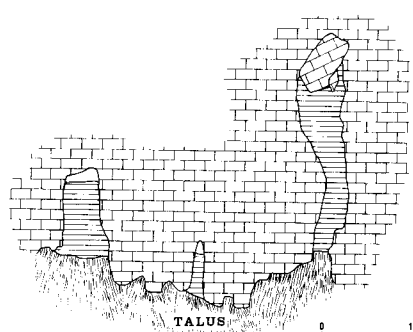


Fig. 25. Sketch of the fissure sediments at Site 4-e of Yage Quarry (drawn on 18 August, 1982).

At Site 4-a, the fissure sediments can be divided into three beds, although the boundaries between them are rather obscure (Fig. 23). The lower bed comprises brown mud with breccia of limestone and chert. Near the southern wall of the fissure, this bed rarely contains breccia of the volcanic ash exposed at Site 3. The middle bed is composed of brown mud which overlies the lower bed with an irregular boundary. The upper bed comprises muddy gravel. The gravel is represented by round pebbles of chert and limestone.

The fissure of Site 4-b is filled with brown mud (Fig. 23).

The fissure sediments of Site 4-c are divided into three beds, namely brown muddy sand (fine alternating beds of brown mud and sand in its upper part), hard brown mud and brown muddy sand in ascending order (Fig. 23). The boundaries between them are indistinct.

The fissure of Site 4-d is the largest in the fissures of Site 4. It is about 5 m wide and about 5 m high. The sediments of this fissure are divided into three beds (1 to 3 in Fig. 24), although these beds are intergradational. Bed 1 is brown mud, and is restricted to a small area in the southern part of the fissure. Bed 2 is brown muddy gravel which is composed mainly of sub-angular to sub-round pebbles. However well-round pebbles are also found in this bed. As regards the gravel composition, chert is predominant, while black slate is subordinate. A thin lens of muddy sand is intercalated in the upper part of this bed. Bed 3 is massive brown mud.

At Site 4-e, three small fissures are observed (Fig. 25). These fissures are filled with brown mud which contains pebble-sized limestone breccia. This mud is identical with Bed 3 of Site 4-d.

Site 5 —

This site seems to correspond to Fissure K of TOMIDA (1978). The fossiliferous fissure is 1.3 to 2.8 m wide and 3.1 m high, and is filled with brown mud and partly with brecciated mud

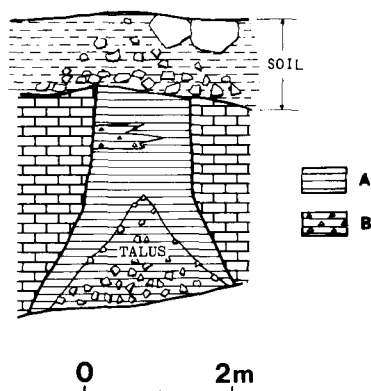


Fig. 26. Schematic sketch showing the fissure sediments at Site 5 of Yage Quarry. A, mud; B, brecciated mud. This figure was drawn in 1977.

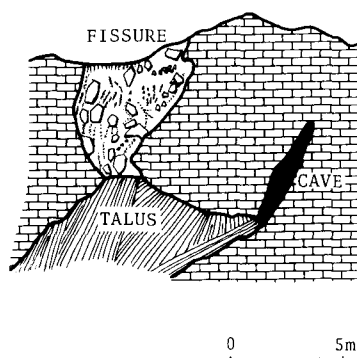


Fig. 27. Schematic sketch of the quarry face at Site 6 of Yage Quarry (drawn in 1976).

(Fig. 26). Fossil bones collected from this mud are dated as $18,040 \pm 990$ yr. B.P. by the ^{14}C method.

Site 6 —

The fossiliferous fissure is exposed on a high quarry face which forms the northeastern corner of the quarry (Figs. 21, 27). It is 1.5 to 5 m wide and about 6 m high. The sediments which fill this fissure are composed mainly of limestone breccia with various size. They are poor in matrix and therefore porous. Because they are dissimilar to the sediments of other sites in lithofacies, both of them are not correlative. Moreover any chronological data on the present sediments are not available. Therefore their geological age is left unknown.

Summary of the fissure sediments in Yage Quarry —

Summarizing up the above description, the fossiliferous sediments of this quarry are classified into the following three groups:

1. Middle Pleistocene sediments (mainly volcanic ash and mud with abundant fish bones)..... Site 1 (most part) and Site 3
2. Late Pleistocene sediments (mainly brown mud and mud with breccia or gravel) Site 1 (partly), Sites 2, 4 and 5
3. Sediments of unknown age (porous breccia) Site 6

6. Suse Quarry (East Fissure)

Small limestone lenses are sporadically distributed in the hilly mountains east of Toyohashi. One of these lenses is quarried by Mitake Mining Company at Suse (Fig. 28). The quarry is formally called "Suse First Quarry" of the company, but generally abbreviated as "Suse Quarry." In this quarry, there were two quarry faces (east and west faces) which surrounded a single quarry floor. In January 1975, MATSUHASHI discovered fossil bones of deer in a fissure exposed on the east face. This fissure called "East Fissure" was situated about

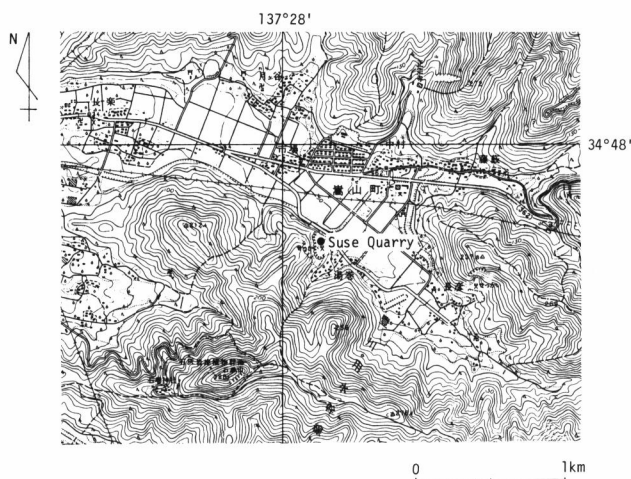


Fig. 28. Index map showing the location of Suse Quarry. The scale 1:25,000 map sheet "Toyohashi" published by the Geographical Survey Institute is used.

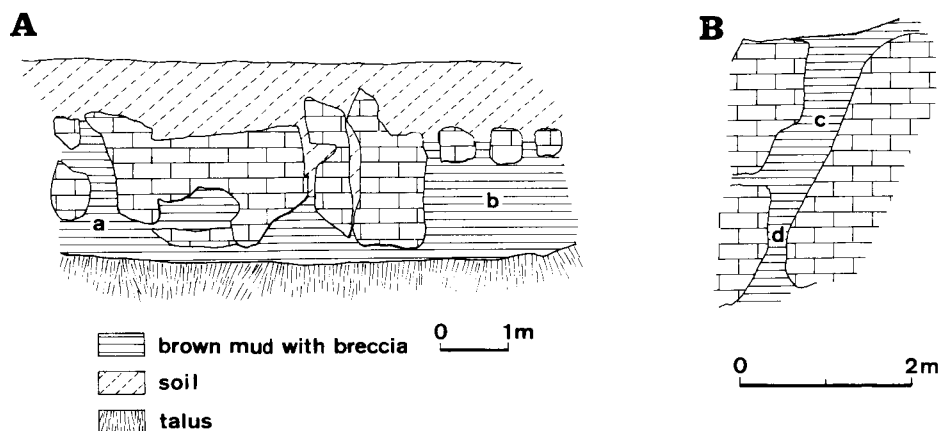


Fig. 29. Explanatory sketch of the fossiliferous fissures in Suse Quarry. Redrawn from the original figure by Y. MATSUHASHI. A, East Fissure; B, West Fissure; a-d, points for the explanation in text.

10 m above the quarry floor and about 2 m below the land surface. MATSUHASHI and his co-operators obtained many vertebrate fossils by the subsequent excavations. Among these fossils, MATSUHASHI (1977) described an antler and mandible of deer, and identified them as an extinct species, *Cervus praenipponicus*.

As shown in Fig. 29, East Fissure is an irregular-shaped fissure, which is filled with brown mud. In the northern part of the fissure (a in Fig. 29), this mud contains gravel in the lower part and a number of deer bones in the upper part. In the southern part (b in Fig. 29), fossils of micro-mammals are abundantly found, while those of deer are rather scarce. Fossil bones collected from this mud is dated as $14,710 \pm 670$ yr. B.P. by the ^{14}C method.

Unfortunately this fissure was completely destroyed by limestone-mining operations until June 1977. Another fossiliferous fissure on the west quarry face (West Fissure) is described in the subsequent section, because its sediments are regarded as Holocene in age.

7. Kannondo Cave Site (Late Pleistocene horizons)

Taishaku-dai, one of the representative karst plateaus in Japan, is situated in the north-eastern part of Hiroshima Prefecture. In the middle of this plateau, the Taishaku River runs from north to south to form a deep valley called "Taishaku-kyo." Many archaeological sites are distributed along the valley. They are collectively called "Taishaku-kyo Sites." These sites usually occupy entrances of limestone caves or rockshelters, and yield a large number of artifacts, human bones and vertebrate remains. Since 1963, they have been continuously excavated by the archaeologists mostly belonging to the Department of Archaeology, Hiroshima University.

Kannondo Cave Site is one of the most important sites in the Taishaku-kyo Sites, which is located in the southern part of the Taishaku-dai Plateau (Fig. 30). Since the discovery of this site (August 1963), the excavations have been carried out almost annually. Their results including the stratigraphy of the sediments and the descriptions of the artifacts are provided in

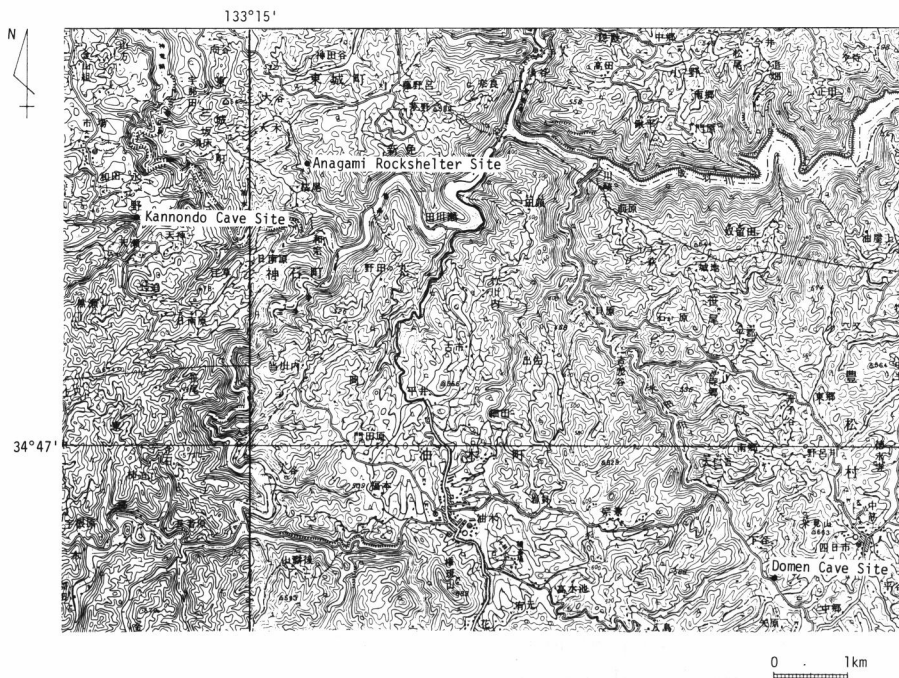


Fig. 30. Index map showing the locations of Domen Cave Site, Anagami Rockshelter Site and Kannondo Cave Site. The scale 1:50,000 map sheets "Yuki" and "Joge" published by the Geographical Survey Institute are used.

the following papers:

OTSUKA (1964)	Tentative excavation in 1963.
FUJITA and KAWAGOE (1965)	First excavation in 1964.
SHIOMI (1968)	Second to forth excavations in each year from 1965 to 1967.
KAWAGOE (1976a)	Fifth to eleventh excavations in each year from 1968 to 1974.
KAWAGOE (1978)	12th and 13th excavations in 1975 and 1976 respectively.
KAWAGOE (1979)	14th excavation in 1978.
KAWAGOE and NAKAGOSHI (1980)	15th excavation in 1979.
FUZINO (1981)	16th excavation in 1980.
KAWAGOE and MIYAHARA (1982)	17th excavation in 1981.
NAKAGOSHI and KOIKE (1983)	18th excavation in 1982.
NAKAGOSHI (1984a)	19th excavation in 1983.
NAKAGOSHI <i>et al.</i> (1985)	20th excavation in 1984.
SUZUKI and NAKAGOSHI (1986)	21th excavation in 1985.

Fourteen excavation grids are decided, which cover most area of this site (Fig. 31). In each grid, the sediments were independently divided into many layers which were named by number in descending order. Therefore, a layer in a grid sometimes differs in horizon from its counterpart in another grid which bears the same number. For example, Layer 19 in Grid GW is not correlative with Layer 19 in Grid D. Hence a chart showing the correlation of the layers among the grids is requested. Although such a chart was already provided by KAWAGOE (1976a) and ISHIDA (1978), more extensive one is tentatively given here (Table 1).

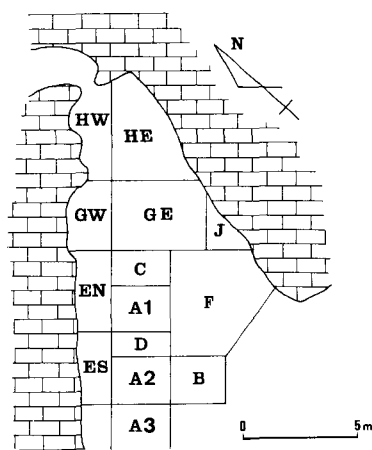


Fig. 31. Plan of Kannondo Cave Site showing the disposition of the excavation grids (simplified from KAWAGOE, 1976a).

As time stratigraphic units, Horizons A to P are proposed to designate each horizon.

As shown in this table, potteries of the Yayoi and later periods are found in Horizons A and B, while those of the Jomon Period are obtained from Horizons B to L. Therefore these horizons approximately correspond to Holocene, and is described in the subsequent section. In the horizons lower than M, however, no potteries occur, and moreover other artifacts become extremely scarce. Because these horizons are undoubtedly assigned to the Late Pleistocene, they are closely described here (Fig. 32).

The sediments of the upper part of Horizon M are composed mainly of mud with breccia, which is brown to yellowish grey in colour. Those of the lower part of the same horizon comprise yellowish grey to greyish white pumice. This pumice bed is traceable into the talus sediments exposed on the cliffs immediately south of Grids A3 and B (Fig. 31). According to OKIMURA *et al.* (1977), the pumice bed is undoubtedly correlative with the Ukinuno Pumice-fall Bed formed by the eruption of Mt. Sanbe. MATSUI and INOUE (1970) determined the age of the Ukinuno Pyroclastic Flow as $16,000 \pm 400$ yr. B.P. by the ^{14}C method. They also mentioned that this pyroclastic flow was almost contemporaneous with the Ukinuno Pumice-fall Bed.

The sediments of Horizon N are composed mainly of dark brown mud with breccia. They contain round gravel in low frequency, and partly intercalate thin beds of calc tufa. In the above-mentioned talus sediments, a thin bed of vitric volcanic ash is observed about 1 m below the pumice bed. SHIBATA (1979) revealed that the ash bed was assignable to the AT Volcanic Ash Layer. The AT is considered to be one of the most important horizon markers in the Japanese Late Pleistocene, which is dated around 21,000 to 22,000 yr. B.P. Because the ash bed in the talus sediments is exactly correlated with the sediments of Horizon N in the excavation grids, this horizon is estimated to be of the same age. Such age estimation is supported by a ^{14}C date of calc tufa sampled from this horizon ($20,150 \pm 300$ yr. B.P. by KOYAMA *et al.*, 1977).

Table 1. Correlation chart showing the relationship among the layers in each grid of Kannondo Cave Site. 1-29, number of layer.

HORIZON	G R I D										CHRONOLOGY
	C	D	ES	EN	F	GW	GE	J	HW	HE	
A	1	1		1	1	1,2					Later than Late Yayoi.
B	2,3			2		3					Later half of Latest Jomon to Early Yayoi.
C	4-7	2	1,2	3-7 II		4,5					Later half of Late Jomon to Latest Jomon.
D	8,9	3	3,4	7 III	2,3	7					Earlier half of Late Jomon.
E	10,11	4	5 upper	7 IV-9 upper	4-8	8					Middle Jomon.
F	12	5,6	5 lower	9 lower		9-12					Later half of Early Jomon.
G	13-16	7-12	6-12	10-16		13-16	13-16				Earlier half of Early Jomon.
H	17,18	13,14	13-16	17,18	12	17,18	17,18				Later part of Earliest Jomon.
I	19	15	17	19		19	19		19	19	Middle part of Earliest Jomon.
J	20	16	18	20	20	20	20		20	20	Early part of Earliest Jomon.
K	21	17	19	21	21	21	21		21	21	Early part of Earliest Jomon.
L	22	18	20	22	22	22	22		22	22	Earliest part of Earliest Jomon.
M (upper)	23	19	21 upper	23	23	23	23 main part 23A		23	23	ca 16000yr.B.P.
M (lower)						23 pumice	23 pumice		23 pumice	23 pumice	
N	24A		21 lower 22	24	24	24A	23B 24B 24A 24C	24B 24C	24	23B 24	20150±300yr.B.P. ca 21000-22000yr.B.P.
O (upper)	25B 25A				25B 25A	25	25B 25A	25B 25A	25	25	31900yr.B.P.
O (lower)							25 lower	25 lower			
P	26B 26A		23 27-29	26B 26A 27-29	26A	26B 26A	26B 26A	26A			

The sediments of the upper part of Horizon O consist mainly of brown mud with breccia, which rarely contains round gravel (but much poorer than in Horizon N). Thin beds of calc tufa are partly intercalated in the sediments. Fossil bones collected from this horizon are dated as 31,900 yr. B.P. by the amino-acid dating method (MATSU'URA, pers. comm.). The sediments of the lower part of Horizon O are composed mainly of yellowish brown mud with



Fig. 32. Sediments of Kannondo Cave Site exposed on the southern walls of Grids GW, GE and J (after KAWAGOE, 1978).

breccia which contains round gravel in low frequency. Thin beds of calc tufa are partly intercalated. The sediments of this part are restricted to Grids GE and J in distribution.

The sediments of Horizon P consist mainly of brown mud with round gravel and limestone breccia. The frequency of round gravel is much higher than in other horizons.

A large amount of the sediments sampled from these horizons were washed on fine-meshed screen (0.5 mm) to collect micro-vertebrate fossils. As the results, a large number of the fossil specimens were obtained. The mammalian fossils collected during the seasons of the excavations as well as by the screening were preliminarily reported by KAWAMURA (1980, 1981, 1982) and KAWAMURA *et al.* (1986). In the present study, these fossils are described in detail, and their faunal characters are also discussed.

8. Locality 2 of Ube Kosan Quarry

This locality is represented by a cave which was called "Maruyama-no-shindo Cave" by HAIKAWA *et al.* (1983). This cave was found on a quarry face of the bench of 147 m in March,

1978 (Fig. 5). Because its entrance* was made by cutting operations of the quarry face, the position of the original entrance is left unknown.

From the entrance, a horizontal passage with widths of 5 to 8 m extends south-eastward (Fig. 33). The sediments deposited on its floor are composed mainly of brown mud, although limestone debris is piled up near the entrance. A small stream dissects these sediments to form a small gorge. The section of the sediments is well observed on the gorge wall. The passage is abruptly changed into an inclined tunnel about 22 m ahead of the entrance. Its floor is covered by numerous fallen blocks of limestone. This tunnel extends eastward in a distance of about 18 m to meet a large hall. This hall has a Λ -shaped plan, and its floor is covered by limestone blocks and muddy sediments.

On 16 March, 1978, the author visited this cave to examine fossiliferous sediments, because he was informed by M. OTA of the occurrence of fossil mammals from this cave a few days before. With co-operation of M. OTA, T. HAIKAWA, A. SUGIMURA, T. NISHIDA and others, he could sample the sediments exposed on the above-mentioned gorge wall (A and B in Fig. 33) to collect micro-vertebrate fossils. On this wall, the following sequence is observed (in descending order; see Fig. 34):

Layer 3: Volcanic ash. Brownish yellow vitric ash is alternated with brown muddy ash. The former ash is finer than the latter. On the lower boundary of this layer, heavy minerals are concentrated to form black bands.

Layer 2: Reddish brown mud. A thin black lens formed by the concentration of heavy minerals is intercalated in the lower part.

Layer 1: Reddish brown muddy gravel. The gravel is well rounded.

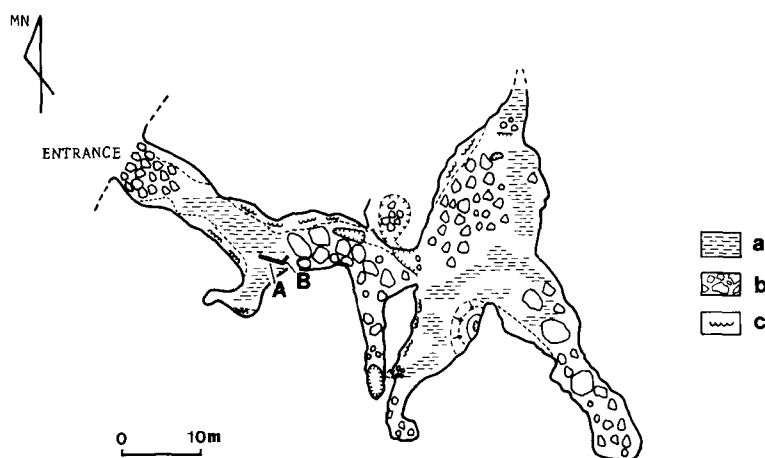


Fig. 33. Plan of Locality 2 of Ube Kosan Quarry (Maruyama-no-shindo Cave). Modified from HAIKAWA *et al.* (1983).

a, mud; b, fallen block; c, flow stone; A, B, two faces of the gorge wall where the section of the cave sediments could be observed.

* It indicates the main entrance shown in Fig. 33. Other two small entrances are recorded by HAIKAWA *et al.* (1983), and they were also opened artificially.

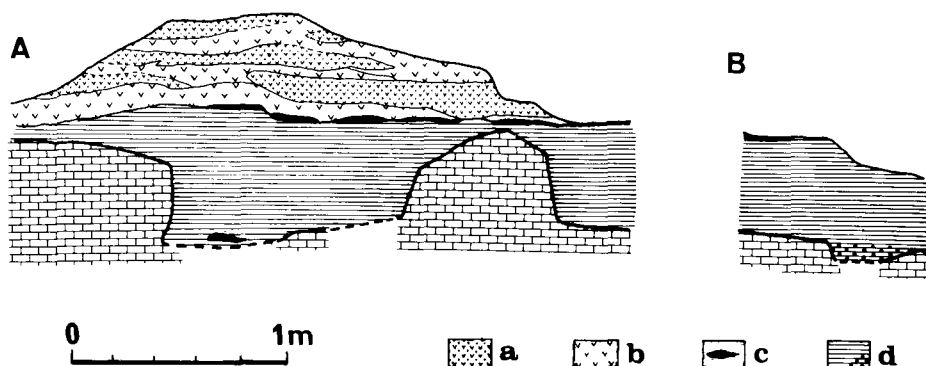


Fig. 34. Cave sediments exposed on the two faces of the gorge wall at Locality 2 of Ube Kosan Quarry (drawn on 16 March, 1978).

A, B, two faces of the gorge wall (see Fig. 33); a, sandy volcanic ash; b, vitric volcanic ash; c, concentrated band of heavy minerals; d, mud (dotted part=muddy gravel).

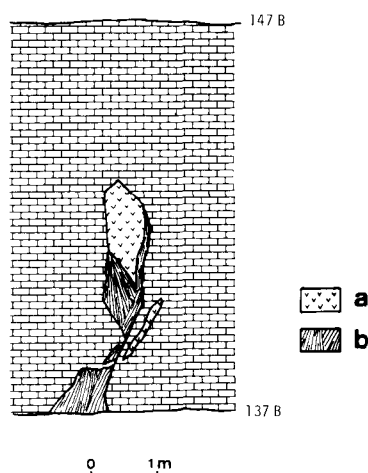


Fig. 35. Diagram showing the fissures filled with volcanic ash on the quarry face of the bench of 137 m near Locality 2 in Ube Kosan Quarry (drawn on 9 February, 1979).

a, volcanic ash; b, talus; 137B, 147B, benches of 137 m and 147 m above sea level respectively.

Similar volcanic ash to Layer 3 was observed to fill two fissures exposed on the quarry faces on the benches of 137 m (Fig. 35) and of 147 m respectively. These fissures are situated near to Locality 2. The lithofacies and heavy mineral composition* suggest that Layer 3 is possibly correlative with the Akiyoshi Volcanic Ash Layer named by TAKAHASHI and KAWANO (1958). The same authors (1970) considered that this ash layer was equivalent to the Aso-4 Pyroclastic Flow, a representative marker bed of the Japanese Late Pleistocene. The age of the Aso-4 was recently estimated as about 70,000 yr. B.P. by MACHIDA *et al.* (1985). Because Layer 3 is well stratified, it is inferred that Layer 3 was originally deposited here or transported from a neighbouring place soon after the original deposition. Therefore this layer is nearly contemporaneous with the Aso-4.

* Analysed by TAKEMURA (pers. comm.).

The mammalian fossils studied here were obtained from Layer 2 by screening. This layer is conformably overlain by Layer 3. Therefore it is most probable that Layer 2 is early Late Pleistocene in age.

9. Seiryukutsu Cave

Hirao-dai, one of the representative karst plateaus in Japan, is situated at the northern end of Kyushu. This plateau is about 400 to 550 m in elevation, and has a rhombic outline elongated in a northeast-southwest direction (Fig. 36). From geological viewpoint, it is composed mainly of massive crystalline limestone which contains no fossils. According to TANAKA *et al.* (1982), 112 caves are known from this plateau. Some of these caves yield the Quaternary vertebrate fossils. Seiryukutsu Cave is the most important of these fossiliferous caves, because fossils of various extinct and exotic mammals were found (NAORA, 1954; HASEGAWA *et al.*, 1980; OKAZAKI *et al.*, 1980; KAWAMURA and SOTSUKA, 1984 etc.).

Seiryukutsu Cave is complicate in structure, which is resulted from the combination of horizontal, vertical and inclined tunnels (Fig. 37). Namely the horizontal tunnels are developed in various levels. They are characterized by strong meandering as pointed by MIYAHISA and KASHIMA (1962). These tunnels are connected with each other by the vertical and inclined tunnels. Because the horizontal tunnel at the lowest level is best developed and

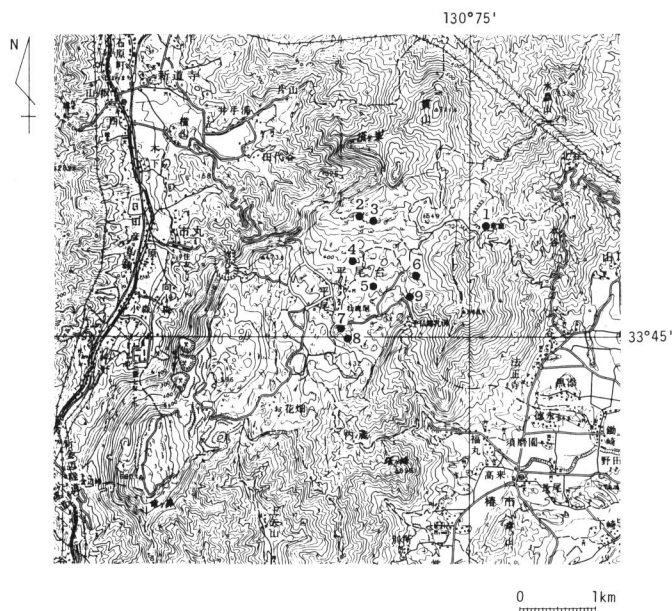


Fig. 36. Index map showing the locations of the fossiliferous caves on the Hirao-dai Plateau described in this paper. The scale 1:50,000 map sheet "Ikuhashi" published by the Geographical Survey Institute is used.

1, Seiryukutsu Cave; 2, Hirao-ana Cave; 3, Ohera-ana Cave; 4, Ninjinkubo First Cave; 5, Yakubono-ana Cave; 6, Mejiro-do Cave; 7, Ojika-do Cave; 8, Oiwa-ana Cave; 9, Yoshigatani Third Cave.

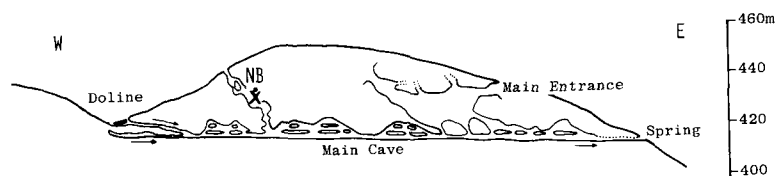


Fig. 37. Section of Seiryukutsu Cave. Simplified from HASEGAWA *et al.* (1980). NB, Naumann Branch. X fossil site.

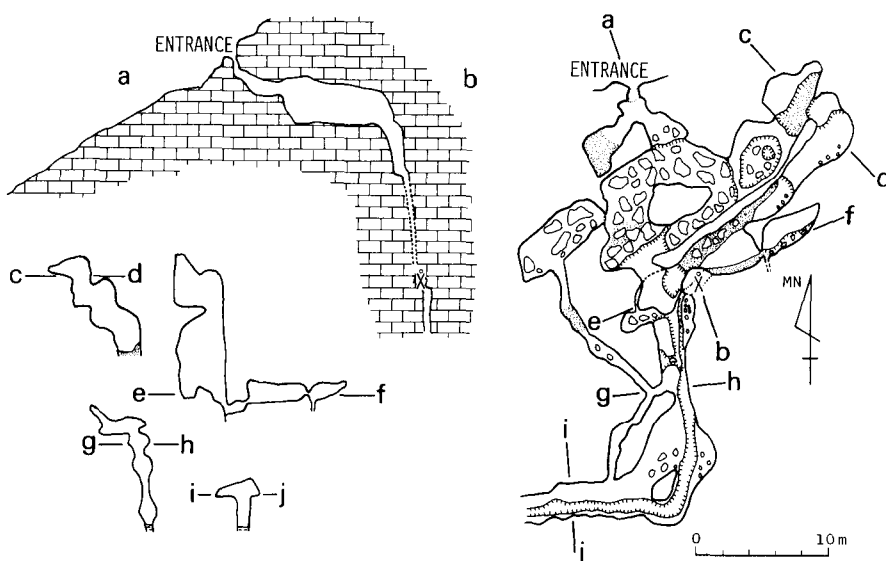


Fig. 38. Detailed plan and section of the Naumann Branch of Seiryukutsu Cave (left figures=section; right figure=plan). Modified from HASEGAWA *et al.* (1980). X fossil site.

largest, it is generally regarded as the main cave of Seiryukutsu Cave (Fig. 37). From the western part of the main cave, a narrow tunnel branches out, and steeply ascends toward the eastern slope of a doline. This tunnel is called "Naumann Branch," and has a complicate structure (Fig. 38). Excepting the fossil tooth of horse recorded by NAORA (1954), all the fossils known from this cave were obtained from the middle of this tunnel.

The fossil materials examined in the present paper were collected from the sediments deposited on the cave floor at the point shown in Fig. 38. The sediments comprise mud with breccia, from which the skull fragments of the elephant (*Palaeoloxodon naumanni*) described by HASEGAWA *et al.* (1980) were obtained. The surface of the sediments is covered by thin travertine. As HASEGAWA *et al.* pointed out, the state of preservation of the fossil elephant suggests that these sediments were not transported from other places, but were originally deposited at this point. The age of the sediments is estimated to be of Late Pleistocene age from the faunal characters.

In a higher level of the Naumann Branch, fossils of the extinct deer (*Sinomegaceros yabei* and

Cervus praenipponicus) were discovered in muddy sediments, and were recorded by SOTSUKA *et al.* (1982). Moreover the molar of *Stegodon orientalis* described by OKAZAKI *et al.* (1980) was collected from the surface of gravelly sediments at a different point. However the relationship among these sediments is unknown.

10. Mejiro-do Cave

This cave is situated near the eastern edge of the Hirao-dai Plateau (Fig. 36). It is the longest horizontal cave in the plateau, and exceeds 1500 m in total length. After sloping down about 20 m south-eastward from the entrance, the cave is divided into three branches (Fig. 39). The first branch extends eastwards, and soon ends about 15 m ahead. The second and third branches comprise the main part of this cave, and extend northwards and southwards respectively. Therefore they are called "northern cave" and "southern cave." The stream in the cave flows down from the southern cave to northern cave. The southern cave is a wide tunnel with widths of 3–8 m. It extends about 120 m ahead from the branching point. In the southern end of this cave, reddish brown mud is deposited on the cave floor. It is more than 0.6 m in thickness, and intercalates several thin layers of gravel. It is assumed that this mud was originally deposited in a fissure above this point, and then redeposited on the floor. The

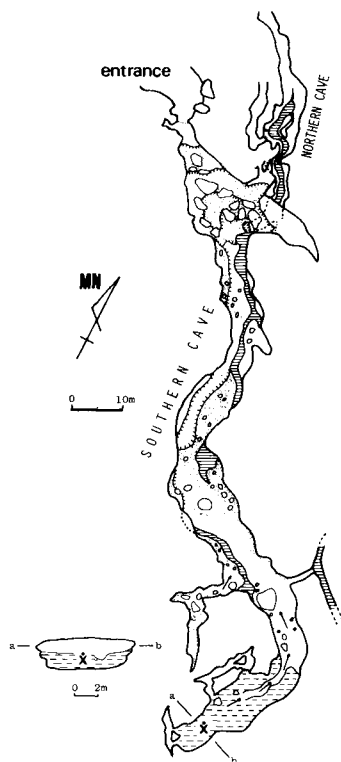


Fig. 39. Plan of Mejiro-do Cave (left bottom figure=section along line a-b). Redrawn from the figure by the Circle of Cave Study, Yamaguchi University. X fossil site.

mammalian remains are obtained from this mud.

The faunal composition, especially the presence of *Sinomegaceros* sp., suggests that the fossiliferous sediments are Late Pleistocene in age. However the fossils are slightly less fossilized than those of Seiryukutsu Cave described above.

11. Minatogawa Site

The Pleistocene limestone called the "Ryukyu Limestone" is widely distributed in the Ryukyu Islands. Numerous caves and fissures are developed in the limestone. They are sometimes filled with fossiliferous sediments. The fossils found in these sediments (and rarely in the limestone itself) have been studied by many palaeontologists (MATSUMOTO, 1926; TOKUNAGA, 1936, 1940; TOKUNAGA and TAKAI, 1939; OTUKA, 1941; HASEGAWA *et al.*, 1973; TAKAI, 1975; HASEGAWA, 1980a *etc.*).

Minatogawa Site is one of these fissures, and is situated about 12 km southeast of Naha (Fig. 40). It is famous for the occurrence of the Pleistocene man. The fissure is exposed on a quarry face with a height of about 10 m in a small limestone quarry (SAKIHAMA's Quarry). In 1967, S. OYAMA discovered mammalian fossils including human bone fragments in the sediments of this fissure. In the subsequent years (1968, 1970 and 1974), systematic excavations were conducted to obtain more complete human bones. The results of the excavations were recently published as a book (SUZUKI and HANIHARA, 1982). Unfortunately, this book does not include the description of the mammalian fossils. As regards these fossils, TAKAI and HASEGAWA (1971) and HASEGAWA (1980a) provided the faunal lists and their brief explanations. Moreover KOWALSKI and HASEGAWA (1976) exclusively described the fossils of rodents, but the

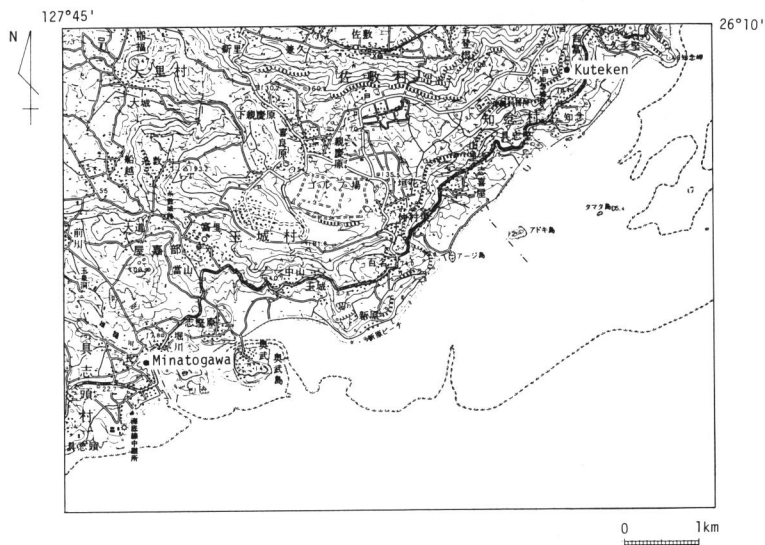


Fig. 40. Index map showing the locations of Kuteken and Minatogawa. The scale 1:50,000 map sheet "Kudakajima" published by the Geographical Survey Institute is used.

systematic descriptions of other taxa have been unpublished.

The present fissure is about 0.6 to 1.0 m in width, and vertically extends from the level of a quarry floor to the top of the quarry face. The bedrock of the fissure comprises the Machinato Limestone (=Minatogawa Limestone) which represents the younger part of the Ryukyu Limestone. The fissure is filled with brown muddy sediments which were briefly described by TAKAI and HASEGAWA (1971). According to them, the following sequence was observed in descending order:

1. Limestone breccia
2. Brown clay with gravel: It contains abundant land shells.
3. Blackish brown mud with numerous bones of bird and boar.
4. Clay with gravel: It contains various vertebrates, and marine and land shells. The human bones were found in this layer.

Charcoal fragments collected from the same horizon as the human bones were dated as $18,250 \pm 650$ and $16,600 \pm 300$ yr. B.P. by the ^{14}C method (SUZUKI, 1975).

The fossil materials examined in the present paper were collected from the sediments possibly belonging to the lowest layer (4) of TAKAI and HASEGAWA's sequence. Therefore they are considered to be of Late Pleistocene age.

12. Kuteken

The fossil locality is situated at a limestone quarry in Kuteken, Chinen (Fig. 40). The Ryukyu Limestone in this quarry is massive, so that caves and fissures are scarcely observed on quarry faces. The fossiliferous sediments were found to expose on an artificial slope in the quarry (Fig. 41). It is inferred that a cave or fissure which was filled with these sediments was mostly destroyed by quarrying operations, but their basal parts were incidentally preserved on the slope.

The sediments are composed of brown muddy breccia, which contains fossils of mammals as well as those of snakes and crabs. These fossils are mostly fragmental. The stratigraphic sequence of the sediments and the mode of occurrence of the fossils are obscure, because the sediments were mostly covered by the debris formed by the quarrying operations. However the faunal composition probably suggests that the sediments are Late Pleistocene in age as discussed in the subsequent chapter (p. 144).

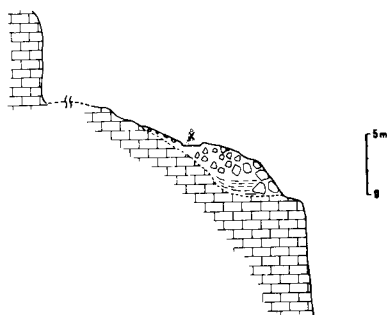


Fig. 41. Schematic cross-section of the fossiliferous sediments at Kuteken. X fossil site. This figure represents the condition observed on 25 December, 1975.

13. Iso

This locality is situated on a small hill, 0.5 km northwest of Iso, Urasoe (Fig. 42). The hill is composed of the Ryukyu Limestone in the upper part and the alternating beds of grey fine sandstone and siltstone of the Mio-Pliocene Shimajiri Group in the lower part. These two geologic units unconformably contact with each other. In November 1975, vertebrate fossils were incidentally found from cave sediments exposed in the upper part of the hill under the construction for disaster prevention. These sediments filled a horizontal cave which was developed in the basal part of the limestone and extended along the unconformity. When the author visited this locality in January 1976, this cave had been mostly destroyed. However he could observe the southern end of the cave remained on a cliff. Moreover the fossiliferous talus which was possibly derived from the original cave sediments was found near the cliff. The fossils examined in the present study were collected from this talus.

OSHIRO and NOHARA (1977) reported the occurrence of fossils of deer and boar from "Iso." Their locality is possibly equivalent to the present locality.

The available data for the age estimation of the sediments are very scarce. Taking the faunal characters into consideration, however, the sediments might be Late Pleistocene in age.



Fig. 42. Index map showing the locations of Iso and Gajanbira. The scale 1:50,000 map sheet "Naha" published by the Geographical Survey Institute is used.

14. Gajanbira

This locality is represented by a small fissure exposed on a high cliff immediately south of Naha Harbour (Fig. 42). Horizontal grey mudstone beds of the Shimajiri Group are observed in the lower part of the cliff (from the base of the cliff to a level of 15 m above sea level). They are unconformably overlain by the Ryukyu Limestone which is exposed in the upper part (from the level of 15 m to the top of the cliff). The present fissure is formed in the limestone (Fig. 43).

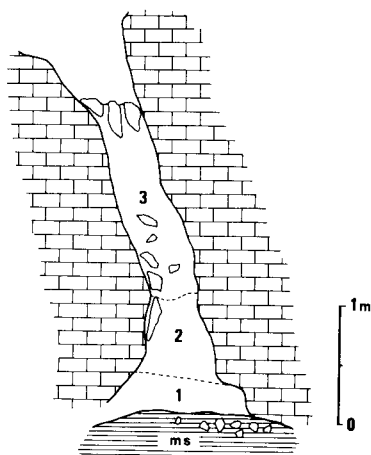


Fig. 43. Sketch of the fossiliferous fissure at Gajanbira. 1-3, fissure sediments; ms, mudstone of the Shimajiri Group. This figure was drawn on 24 December, 1975.

The fissure is 3.5 m in height and 0.5 m in width. It strikes N40°W, and steeply dips south-westward. The sediments which fill the fissure can be divided into the following three layers (described in descending order):

Layer 3 (1.5 m in thickness): Loose brown mud with limestone breccia. It yields abundant land shells, and rarely contains marine shells.

Layer 2 (0.75 m in thickness): Brown mud with land shells. The shells are highly concentrated. This layer contains abundant fossils of mammals, snakes, frogs and crabs. Additionally it rarely yields marine shells.

Layer 1 (0.5 m in thickness): Dark brown mud with breccia of cave limestone. This layer is barren of fossils.

Excepting three specimens of the OSHIRO Collection, all the materials examined in the present study were collected from Layer 2 by screening. On the other hand, NOHARA (1972) and OSHIRO and NOHARA (1977) reported the occurrence of fossil vertebrates from this locality. These fossils were assigned to deer, boars, birds, turtles and snakes, but the exact horizon of their occurrence was not recorded.

Because of the scarcity of available data for dating, it is difficult to determine the geological age of these sediments. In the present study, the sediments are tentatively assigned to the Late Pleistocene on the basis of the faunal composition.

C. Holocene localities

1. Suse Quarry (West Fissure)

In June 1975, Y. MATSUHASHI found a fossiliferous fissure on the west quarry face of Suse Quarry. It is called "West Fissure," which was filled with brown mud (Fig. 29). According to him, fossil bones of middle-sized mammals were concentrated in the upper part of the mud (c in the same figure), while those of micro-mammals were obtained from its lower part (d). In March 1976, this fissure was completely destroyed by the progress of the mining operations.

The fossils from this fissure are less fossilized than those from East Fissure of the same quarry. They are also poorer in fluorine content than the latter (MATSU'URA, pers. comm.). Their fluorine content indicates that the sediments of West Fissure are possibly assigned to the Early Holocene. Such age estimation is consistent with their faunal composition.

2. Kitoragawa Site

So-called "Kawachi Plain" is a wide alluvial plain on the east of Osaka. This plain is formed by the Holocene sediments such as soft mud, sand and gravel. These sediments are about 20m in maximum thickness. They are of marine origin in the lower part, and of fluvio-lacustrine origin in the lowest and upper parts. Their depositional history was explained in detail by KAJIYAMA and ITIHARA (1972).

Kitoragawa Site is situated in the eastern margin of the Kawachi Plain (Fig. 44). It was incidentally discovered by the road construction in 1963, where several artifacts were obtained from the fluvio-lacustrine sediments of the upper part. In 1976, the excavation of this site was carried out by the archaeologists of the Association for the Preservation of Archaeological Sites, Higashi-osaka City. Several excavation pits were dug to examine the cultural layers. The

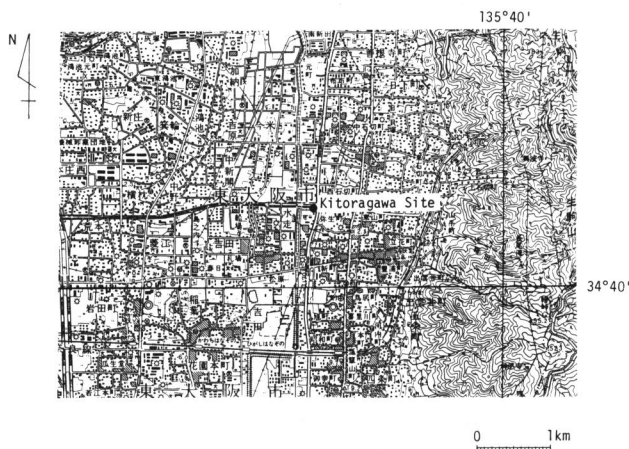


Fig. 44. Index map showing the location of Kitoragawa Site. The scale 1:50,000 map sheets "Osaka-tohokubu" and "Osaka-tonanbu" published by the Geographical Survey Institute are used.

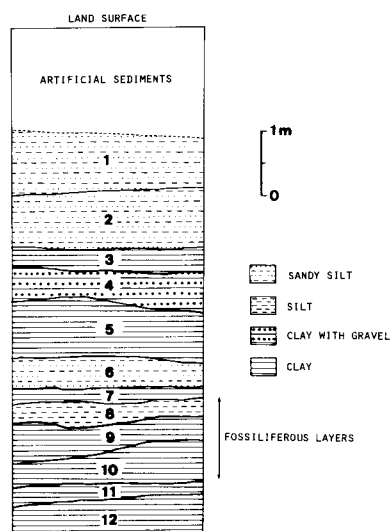


Fig. 45. Explanatory sketch of the northern wall of the excavation pit of Kitoragawa Site. Redrawn from the original figure by the Association for the Preservation of the Archaeological Sites, Higashiosaka City. For detailed explanation of each layer see text.

section of the sediments were observed on the walls of these pits. A representative section is shown in Fig. 45, where the following sequence is observed in descending order:

- Layer 1: Light bluish grey sandy silt.
- Layer 2: Dark bluish grey sandy silt.
- Layer 3: Dark bluish grey clay.
- Layer 4: Dark grey clay with gravel.
- Layer 5: Black clay.
- Layer 6: Greyish brown sandy silt.
- Layer 7: Dark greyish brown clay.
- Layer 8: Black silt.
- Layer 9: Light yellowish grey clay.
- Layer 10: Dark grey clay.
- Layer 11: Dark bluish grey clay.
- Layer 12: Bluish grey clay.

Layers 8, 9 and 10 yield potteries of the Yayoi Period as well as vertebrate remains. They are approximately dated as 2000 yr. B.P. from the archaeological evidence. A large amount of the sediments were sampled from these layers to collect micro-vertebrate remains by the screening method. In addition to the materials obtained by this method, the mammalian remains directly collected from the sediments during the seasons of the excavation are also examined in the present study.

3. Domen Cave Site

Domen Cave Site is an archaeological site belonging to the Taishaku-kyo Sites, which is situated about 10 km east-southeast of Kannondo Cave Site (Fig. 30). This site was discovered and tentatively excavated in August 1964. The subsequent excavations of fifteen times revealed that this site was one of the most important sites in the Taishaku-kyo Sites, and yielded numerous artifacts, human bones and other vertebrate remains mainly of the early part

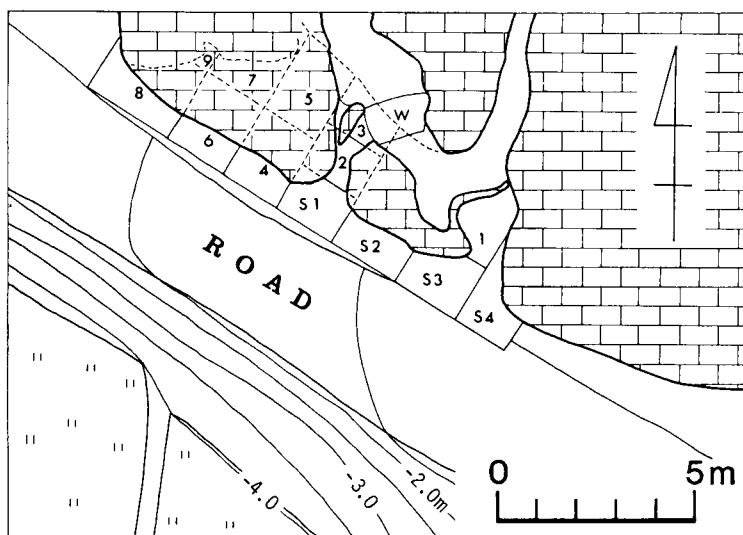


Fig. 46. Plan of Domen Cave Site showing the disposition of the excavation grids (after NAKAGOSHI, 1984c).

of the Jomon Period. The reports on these excavations appear in the following literatures, which deal with the stratigraphy of the sediments and the descriptions of the artifacts and remains:

- | | |
|------------------------|---|
| SHIOMI (1965)..... | Tentative excavation in 1964. |
| FUKUI (1968)..... | First and second excavations in 1967 and 1968 respectively. |
| KAWAGOE (1976b)..... | Third, fourth, fifth and sixth excavations in 1969, 1970, 1972 and 1973 respectively. |
| KAWASE (1978a)..... | Eighth and ninth excavations in 1976 and 1977 respectively. |
| KAWASE (1979)..... | Tenth excavation in 1978. |
| NAKAGOSHI (1980)..... | Eleventh excavation in 1979. |
| KAWAGOE (1981)..... | Twelfth excavation in 1980. |
| NAKAGOSHI (1982)..... | 13th excavation in 1981. |
| NAKAGOSHI (1983)..... | 14th excavation in 1982. |
| NAKAGOSHI (1984c)..... | 15th excavation in 1983 (final excavation). |

Unfortunately the report on the seventh excavation has been hitherto unpublished.

The disposition of the excavation grids is shown in Fig. 46. Because layer numbers in each grid is partly inconsistent as in Kannondo Cave Site, a correlation chart is made on the basis of the descriptions of the above-listed literatures (Table 2). In this table, six horizons (Horizons I to VI) are proposed as time stratigraphic units. Based on the literatures, the following brief descriptions are given to the sediments of each horizon:

The sediments of Horizon I are composed mainly of black to blackish brown earth with breccia, which intercalates an ash bed in the lower part. Those of Horizon II consist of dark grey ash, while those of Horizon III are composed mainly of dark brown to brown mud with breccia. The latter sediments partly intercalate thin beds of ash and burned earth.

The sediments of Horizon IV consist of dark brown to greyish brown mud with breccia,

Table 2. Correlation chart showing the relationship among the layers in each grid of Domen Cave Site. 1-15, number of layer.

Grid Horizon	1,S3	2,3,S1	S2	4	5	6	7	8,9	Period
I	1-3	1- 2 upper							Later than Yayoi
II	4	2 lower							Latest Jomon
III	5	3-4	1- 7 upper						Late Jomon
IV	6-9	5-8	7 lower- 12 upper	8-9					Early Jomon
V	10-14	9- 12 lower	12 lower -13	10- 12 lower	10- 12 lower	10- 12 upper	10- 12 upper	10- 12 upper	Earliest Jomon
VI	15	13-14		13- 14 lower	13-14	13-14	13	13	Earlier than Earliest Jomon

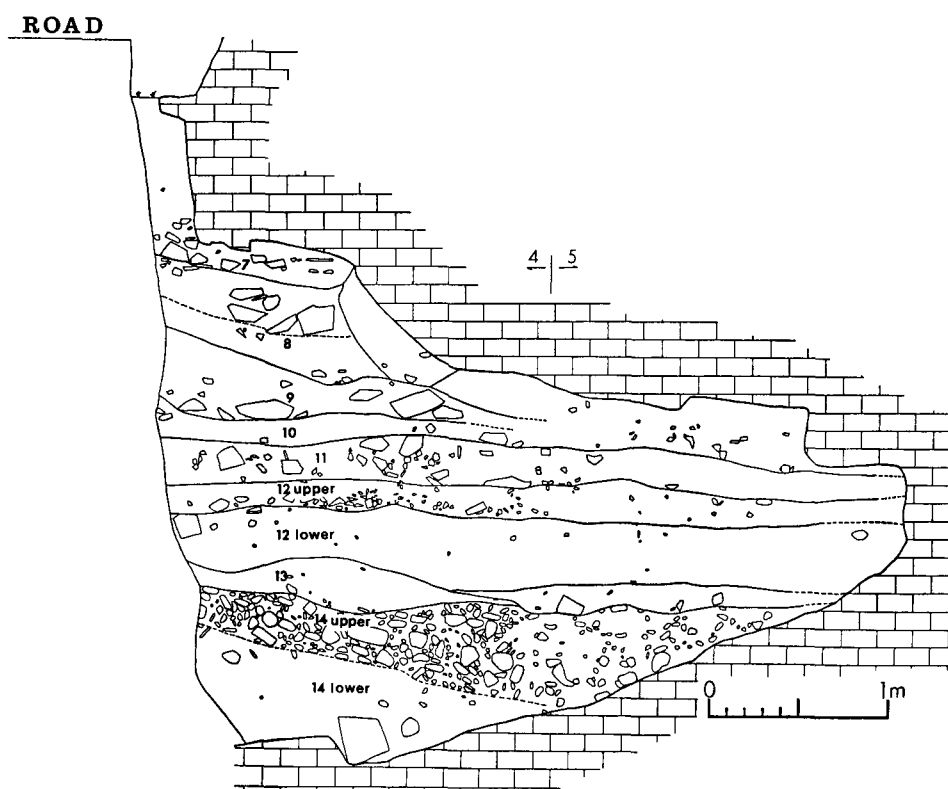


Fig. 47. Cross-section of the sediments of Domen Cave Site along the eastern walls of Grids 4 and 5 (after KAWASE, 1978a).

whose lowest part becomes a thick ash bed in Grids S-1, 2 and 3. Moreover they partly contain calc tufa. The sediments of Horizon V consist mainly of dark brown mud with breccia, which contain round gravel and calc tufa in low frequency. Additionally, a few thin ash beds are partly intercalated. In Grids 4, 6 and 8, a shell bed with a maximum thickness of 25cm is observed in the upper part of this horizon. It contains a large amount of fresh-water molluscs and animal bones. The sediments of Horizon VI is composed mainly of reddish brown muddy sand and gravel which partly grade into coarse sand with round gravel. They are considered to be of fluvial origin.

Mammalian remains were obtained from all the horizons except VI, but especially abundant in V. Of these, the remains collected in the field seasons of the tentative, first to seventh, ninth and tenth excavations are examined in the present study. Moreover a large amount of the sediments were sampled from Horizon V in the seasons of the 13th to 15th excavations to wash by fine screen (0.5 mm mesh). As the result of the screening, many micro-mammalian remains were obtained, which are also examined here.

4. Anagami Rockshelter Site

Anagami Rockshelter Site, an archaeological site in the Taishaku-kyo Sites, is situated about 2.5 km east-northeast of Kannondo Cave Site (Fig. 30). It was discovered by the archaeologists of Hiroshima University in October 1977. The discovery was followed by the tentative excavation in the same month which revealed the occurrence of the Jomon potteries from the sediments of the site. From 1980 to 1984, systematic excavations were annually conducted to obtain more artifacts and to confirm the stratigraphy of the sediments. The reports on these excavations are provided in the following papers:

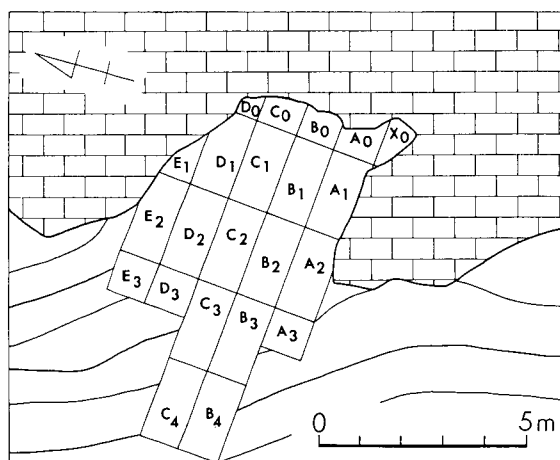


Fig. 48. Plan of Anagami Rockshelter Site showing the disposition of the excavation grids (after NAKAGOSHI and SUZUKI, 1985). Contour lines are drawn at intervals of 50 cm.

KAWASE (1978b).....	Tentative excavation in 1977.
NAKAGOSHI (1981).....	First excavation in 1980.
FURUSE (1982).....	Second excavation in 1981.
FURUSE (1983).....	Third excavation in 1982.
NAKAGOSHI (1984b).....	Fourth excavation in 1983.
NAKAGOSHI and SUZUKI (1985).....	Fifth excavation in 1984 (final excavation).

As shown in Fig. 48, 22 grids were decided for the excavations. The eastern grids (X-0, A-0, B-0, C-0, D-0, A-1, B-1, C-1, D-1 and E-1) occupy a floor of a rockshelter, so that they are roofed by an overhanging wall of bedrock (Fig. 49). The western grids (remaining grids) are open, and are disposed on a gentle slope dipping south-westward. Based on the above-listed papers, the following descriptions are given for the sediments of the site.

Because the basement rock rises near the land surface along the western borders of A-1 and B-1 as well as in the northern parts of B-0 and B-1, the sediments in the southern half of the rockshelter (Grids A-0, A-1, B-0 and B-1) are discontinuous to those of other grids (Fig. 49). They are deposited in a small pocket, and show the following sequence (described in descending order):

Layer 1 (5–10 cm in thickness): Dark brown soil.

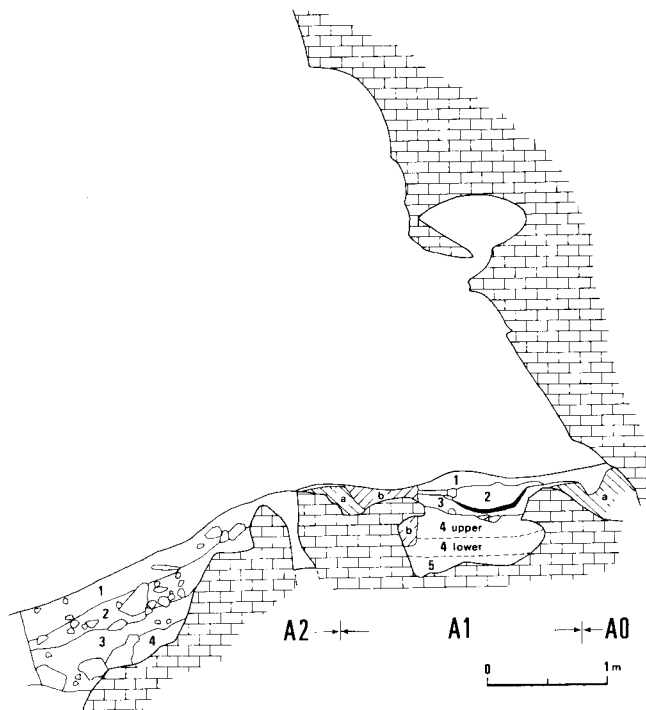


Fig. 49. Cross-section of the sediments of Anagami Rockshelter Site along the northern walls of Grids A-0, A-1 and A-2 (partly modified from NAKAGOSHI, 1981). 1–5, number of layer (the layers in Grids A-0 and A-1 do not correspond to those in Grid A-2; see text); a, unclassified strata; b, disturbed sediments.

Table 3. Correlation chart showing the relationship among the layers in the western grids of Anagami Rockshelter Site. The sequence in the grids of the fifth excavation is regarded as the standard.

Fifth Excavation (Grids B-3, C-3, C-4 and D-3)	First Excavation (Grids A-2, and B-2)	Second Excavation (Grid B-2)	Third Excavation (Grids C-2, A-3, B-3 and C-3)	Fourth Excavation	
				(Grids C-2, A-3, B-3 and C-3)	(Grid B-4)
Layer 1	1	1	1	1	1
Layer 2	2	2	2	2	2
Layer 3A Layer 3B	3	3	3 upper	3	3
Layer 4			3 lower	4	4?
Layer 5	4		4	5	

Layer 2 (20 cm in maximum thickness): Ash layer which is considered to be the Middle Ages or later.

Layer 3 (10–20 cm in thickness): Dark brown mud with round gravel. Potteries of the Late Jomon Period are obtained from the lower part.

Layer 4 (45 cm in maximum thickness): Brown to greyish brown mud with limestone breccia. Potteries of the Late Jomon Period are obtained.

Layer 5 (about 20 cm in thickness): Light brown mud which is assigned to the Early to Earliest Jomon Period.

Layer 6 (about 5 cm in thickness): Yellowish brown mud without artifacts.

In Grid X-0, the sediments fill another small pocket, so that they are also discontinuous to those of other grids. The following sequence is observed in this grid (described in descending order):

Layer 1 (about 10 cm in average thickness): Dark brown soil with potteries of Haji-type and of the Middle Ages.

Layer 2 (about 20 cm in maximum thickness): Dark yellowish brown mud with potteries of Haji-type.

Layer 3 (about 10 cm in maximum thickness): Light yellowish brown mud with potteries of Haji-type and of the Late Jomon Period.

The sediments in the western grids (A-2, B-2 ... E-2; A-3, B-3 ... E-3; B-4 and C-4) have the most perfect sequence in this site. They are divided into several layers which are named by number in descending order as in other grids. Because the numbers of the layers are not always consistent in each grid, a correlation chart is given in Table 3. Designated by the numbering system of the fifth excavation as the standard, these sediments are described as follows:

Layer 1 (10–40 cm in thickness): Blackish brown soil with the Haji-type potteries. It also contains the Jomon potteries in low frequency.

Layer 2 (20–50 cm in thickness): Dark brown mud with breccia. It contains potteries of the Haji-type and of the Jomon Period.

Layer 3A (including Layers 3 and 3-upper in the reports of the first to fourth excavations; 15–60 cm in thickness): Greyish or light brown mud with breccia. Potteries of the Early Jomon Period mainly occur, but those of the Haji-type and of the Late Jomon Period are rarely found.

Layer 3B (about 50 cm in thickness): Light brown mud with breccia. This layer yields potteries of the Early Jomon Period.

Layer 4 (including Layer 3-lower in the report of the third excavation; 30–60 cm in thickness): Light brown mud with breccia and calc tufa. This layer yields potteries of the Earliest Jomon Period, but partly contains those of the Early Jomon Period.

Layer 5 (including Layer 4 in the reports of the first and third excavations; 20–100 cm or more in thickness): Yellowish brown mud. It partly contains sand, breccia and round gravel. No artifacts are found except in the uppermost part.

In the northern part of the rockshelter (Grids C-0, C-1, D-0, D-1 and E-1), the sediments are thin and mostly disturbed. Therefore it is generally difficult to correlate them with the sediments of other grids. The stratigraphic sequence observed in Grid C-1 in the second excavation represents those of these grids. It is described in descending order as follows:

Layer 1 (20 cm in maximum thickness): Greyish or blackish brown soil which contains not only artifacts of the Modern Ages but also potteries of the Jomon Period. This layer was renamed "Layer a" in the third excavation.

Layer 2 (20 cm in maximum thickness): Greyish or dark brown mud which contains potteries of the Jomon Period. This layer was also renamed "Layers b and c" in the third excavation.

Layer 3 (40 cm in maximum thickness): Yellowish brown mud. This layer corresponds to Layer 4 in the above-mentioned western grids.

Layer 4 (45 cm in maximum thickness): Yellowish grey mud without artifacts.

The mammalian remains examined in the present study were collected in the first excavation from all the layers of the southern half of the rockshelter (Grids A-0, A-1, B-0 and B-1), and Layers 1 and 2 of the western grids (A-2 and B-2). These remains were preliminarily reported by KAWAMURA (1983). Additionally the sediments from Layer 3 of Grid B-2 were washed by screens of 0.5 mm mesh to collect micro-vertebrate remains in the second excavation. The specimens obtained by this method are also examined here.

5. Kannondo Cave Site (Holocene horizons)

Because the Late Pleistocene horizons are already described in the preceding section, a brief description of the Holocene horizons (A to L) is exclusively given here (see Table 1 and Fig. 32).

The sediments of these horizons are composed mainly of mud or earth with many intercalations of ash and burned earth, and are generally dark brown, brown or dark grey in colour. Potteries are abundantly found in all the horizons. They are very useful for the dating of the sediments. Each horizon is archaeologically dated as shown in Table 1.

The sediments yield abundant mammalian remains as well as human bones. Of these, non-human remains were preliminarily reported by TANAKA (1976), ISHIDA (1978) and KAWAMURA (1978, 1979a). In the present study, these remains are re-examined.

6. Tanuki-ana Cave

Tanuki-ana Cave is a small inclined cave which opens on the southern part of the Akiyoshi-dai Karst Plateau (Figs. 4, 50, 51). This cave is about 28 m in maximum length and about 9 m in maximum width. From the entrance, a narrow passage extends eastward (Fig. 52). A small vertical pit is observed on the ceiling of the passage. It communicates with the land surface. The floor of the passage slopes down with angles of 20–30°. Muddy sediments are deposited on the floor, and become gravelly inward. At the points of 10–14 m ahead of the entrance, the passage becomes broader and grades into a hall. The floor of the hall also dips inward, but its inclination is gentler than that of the passage. In the western part of the hall, the floor is covered by numerous limestone breccia and fallen blocks, while it becomes muddy in the eastern part. The hall abruptly tapers to be a narrow tunnel at the point of 20 m inward from the entrance. This tunnel extends south-eastward, and terminates 8 m ahead.

The result of the speleological survey of this cave was first published by TAKAHASHI and KAWANO (1957). They dug a trench with a depth of about 1 m (Fig. 52, D), and discovered several fossils of mammals and land shells. In the next year, SHIKAMA and OKAFUJI (1958) identified these fossils, and gave an explanation to the stratigraphy of the sediments observed in the trench. These authors mentioned that the mammalian fossils were mostly obtained from brown clay 5–20 cm below the surface which was assigned to their "Akiyoshi brown clay bed." They considered that this clay bed was Late Pleistocene in age.

In order to re-examine the stratigraphy of these authors, the excavation team headed by the present author again excavated the sediments of the cave in the following six field seasons from 1976 to 1981:

First excavation	26 and 29 February, 1976.
Second excavation	23 to 28 October, 1977.
Third excavation	17 to 22 March, 1978.
Fourth excavation.....	20 to 27 June, 1981.
Fifth excavation.....	13 to 29 August, 1981.
Sixth excavation	17 to 23 October, 1981.

The trench shown as C in Fig. 52 was excavated in the first excavation. On the other hand, the subsequent excavations were carried out in Grids A and B of the same figure.

The results of the first to third excavations were preliminarily reported by KAWAMURA and TAMIYA (1980), who described the stratigraphic sequence of the sediments from the surface to a depth of 125 cm, and listed the mammalian fossils obtained from each horizon. Moreover, on the basis of the archaeological and faunal evidences, these authors inferred that the "Akiyoshi brown clay bed" in this cave was assignable to Holocene. On the other hand, the fourth to sixth excavations revealed the sequence of the deeper part (125 to 240 cm in depth) and its faunal composition. In addition, fossil bones collected from this part were dated by the ^{14}C method. The result of the dating strongly supports the age estimation by KAWAMURA and TAMIYA (1980).

Summarizing up the results of all the excavations, the following description is given to the stratigraphic sequence of the sediments (Figs. 53, 54):

Layer 1: Black to dark brown loose mud with limestone breccia. The detailed description is given

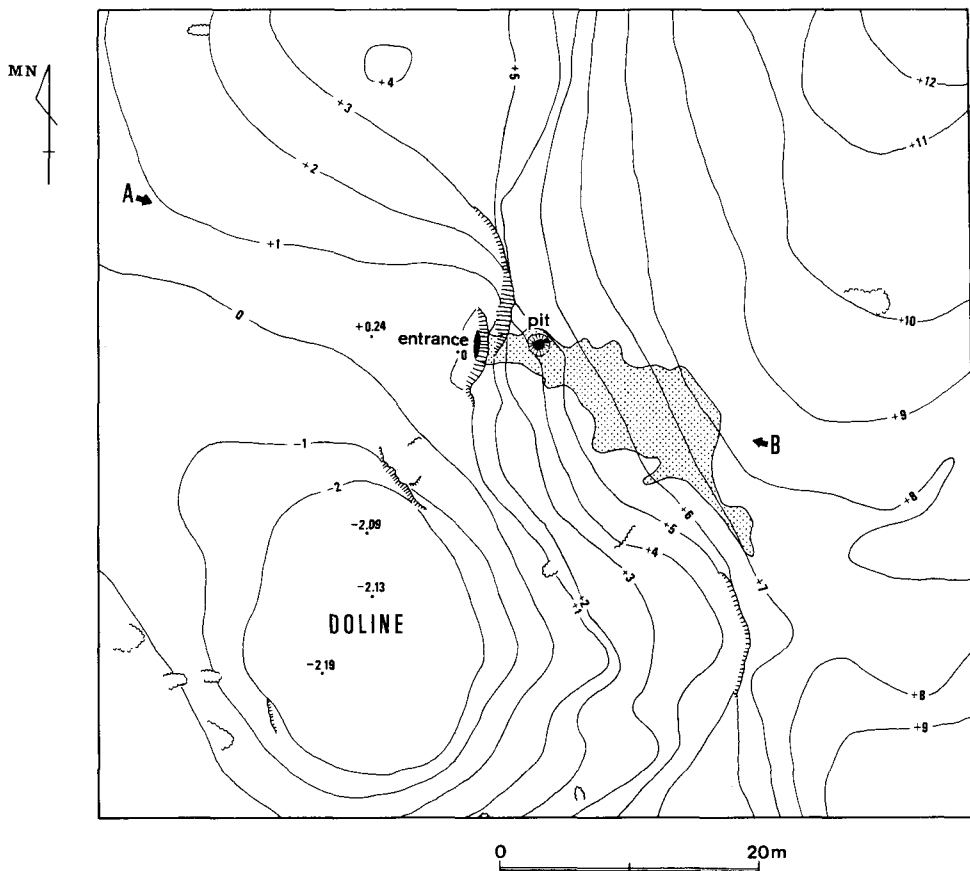


Fig. 50. Contour map showing the location of Tanuki-ana Cave and the topography around it.

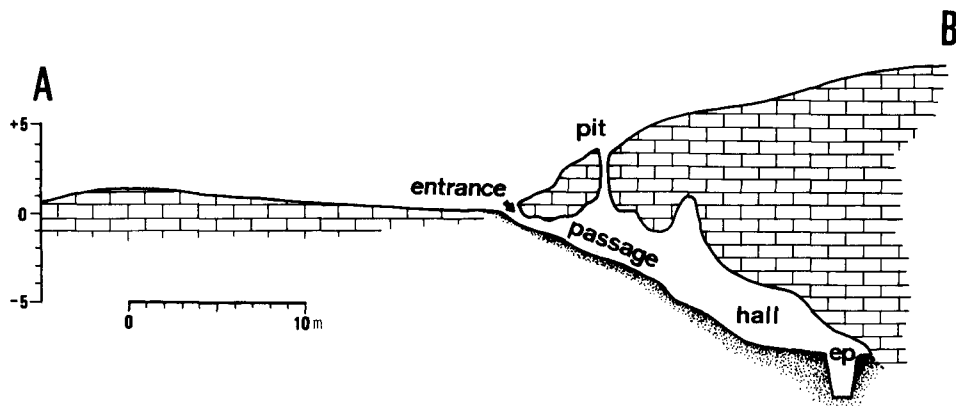


Fig. 51. Cross section of Tanuki-ana Cave along line A to B in Fig. 50. ep, excavation pit.

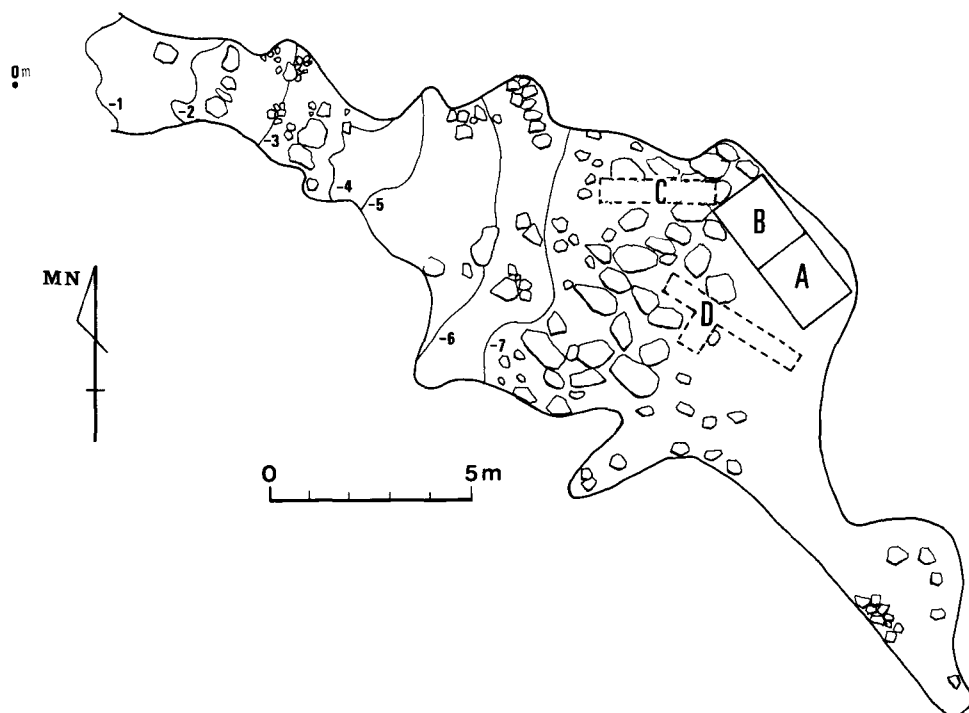


Fig. 52. Plan of Tanuki-ana Cave. A, B, grids of the excavation pit for the second to sixth excavations; C, trench of the first excavation; D, trench of the excavation described in TAKAHASHI and KAWANO (1957).

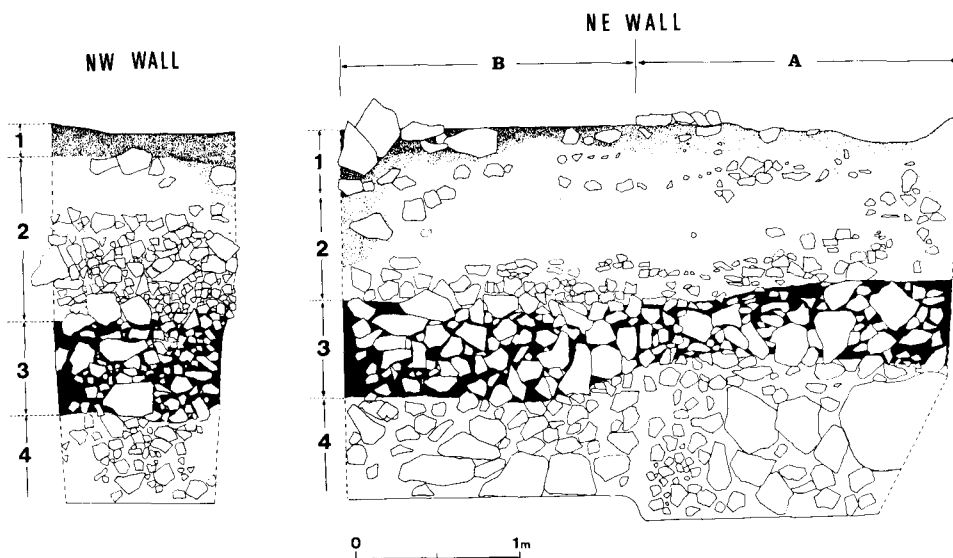


Fig. 53. Detailed sketch of the northwestern wall (left-hand figure) and northeastern wall (right-hand figure) of the excavation pit in Tanuki-ana Cave. A, B, grids shown in Fig. 52; 1-4, layer.

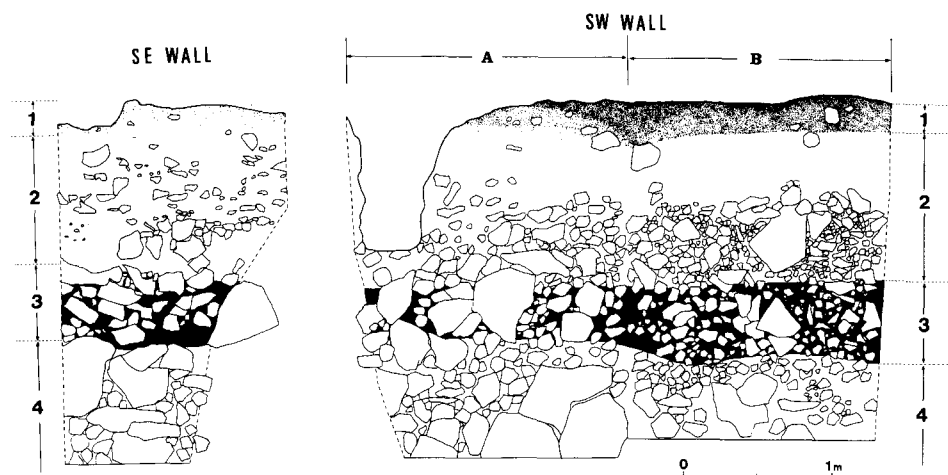


Fig. 54. Detailed sketch of the southeastern wall (left-hand figure) and southwestern wall (right-hand figure) of the excavation pit in Tanuki-ana Cave. A, B, grids shown in Fig. 52; 1-4, layer.

in KAWAMURA and TAMIYA (1980).

Layer 2: Brown compact mud with limestone breccia, which is also closely described in the same paper. Stone implements of the Early Jomon Period were discovered in the lower part. This layer grades into Layer 3.

Layer 3: Limestone breccia bed with muddy matrix. The matrix is so poor that the layer is porous in appearance. The breccia attains to 50cm in maximum diameter. A marine shell is obtained from the lower part. It seems to be transported by human activity. This layer also grades into Layer 4.

Layer 4: Muddy breccia or mud with abundant breccia. The breccia consists of limestone only, and attains to 70 cm in maximum diameter. The mud which constitutes the matrix of the breccia is brown and sticky. A ^{14}C age of fossil bones from this layer is determined as 7580 ± 250 yr. B.P.

In spite of SHIKAMA and OKAFUJI's age estimation, all of the layers are undoubtedly assigned to Holocene.

In accordance with the sequence, the sediments were divided into 13 horizons for sampling (Table 16). Each horizon represents 10-20 cm in thickness. The sediments collected from each horizon were washed by screens of 0.5 mm mesh. As the results, a large number of vertebrate fossils (mainly micro-mammals) were obtained from all the horizons. In addition to the materials directly collected from the sediments in the field seasons, these fossils were examined in detail. The faunal characters obtained by the examination will be described in Chapter V.

7. Husen-ana (Fusen-ana) Cave

This cave opens about 0.6 km northeast of the main entrance of Shuho-do (Akiyoshi-do) Cave which is the most famous cave in Japan (Fig. 4). The report on the speleological exploration of the cave was first published by TAKAHASHI and KAWANO (1957). They provided a plan and sections, and explained the morphology of the cave. Moreover they noticed the

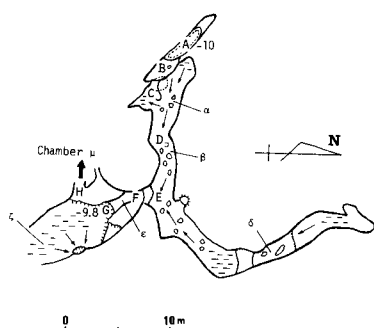


Fig. 55. Plan of Husen-ana Cave (simplified from the figure by KAWANO *et al.*, 1973). A–H, α , β , δ , ϵ , ζ , μ ; names for point, pit, tunnel, fissure and chamber. These names are cited from SHIKAMA and OKAFUJI (1958, Text-fig. 3).

occurrence of mammalian fossils including elephant and giant deer. In the next year, SHIKAMA and OKAFUJI described these mammals, and gave an explanation to the stratigraphy of the sediments which yielded them. In 1973, KAWANO *et al.* renewed the plan and section of the cave on the basis of their own explorations.

According to these previous authors, this cave is very complicate in structure, and comprises vertical pits, fissures, narrow inclined tunnels and a wide chamber. As shown in Fig. 55, from the entrance (A), a vertical pit with a depth of 10 m leads us to the first terrace (B). An inclined tunnel (α and β) extends eastward in a distance of 10 m. A short branch (C) is connected to this tunnel near the entrance. On the cave floor between D and E, SHIKAMA and OKAFUJI (1958) obtained cervid bones. At E, the tunnel β meets a branch (δ) which extends northward. Through a narrow tunnel (ϵ), we reach a large fissure (ζ). Another narrow tunnel opens on the western wall of this fissure at H. It leads us to a large chamber (μ). A deep pit opens at the middle distance of this tunnel, where SHIKAMA and OKAFUJI found remains of racoon dog. These authors also reported the occurrence of several extinct mammals (elephant, giant deer, wolf etc.) from the floor of Chamber μ .

In 1972, K. NAKAGAWA and the members of the Nagato Caving Club sampled brown mud deposited on the cave floor at C. They screened it to collect vertebrate fossils. By their courtesy, the present author could examine the fossils which they obtained*. These fossils are slightly fossilized, and possibly assigned to Holocene. Their faunal composition is also consistent with such age estimation.

8. Fossiliferous caves on Hirao-dai

Nine fossiliferous caves on the Hirao-dai Karst Plateau are described in the present paper. Of these, Seiryukutsu Cave and Mejiro-do Cave are already described in the preceding section, because the fossiliferous sediments of these caves are assigned to the Late Pleistocene. However the mammalian remains from other seven caves are considered to be Holocene age from the state of fossilization and faunal characters.** These caves are Hirao-ana Cave,

* Their collection is now stored in the Akiyoshi-dai Museum of Natural History.

** The detailed explanation is given in Chapter V.

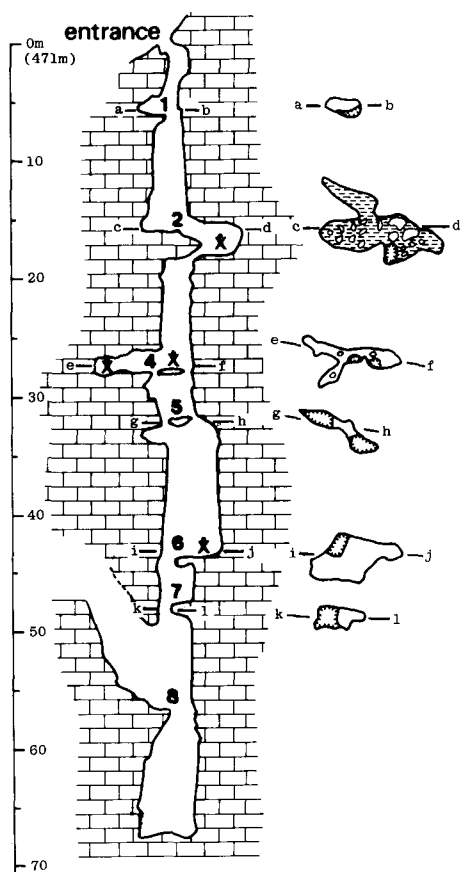


Fig. 56. Section (left figure) and plan (right figures) of Hirao-ana Cave. Redrawn from the figure by the Kitakyushu Caving Club. The scale on the left side indicates the depth of the cave (entrance=471 m above sea level).

1-8, number of terrace; X fossil site.

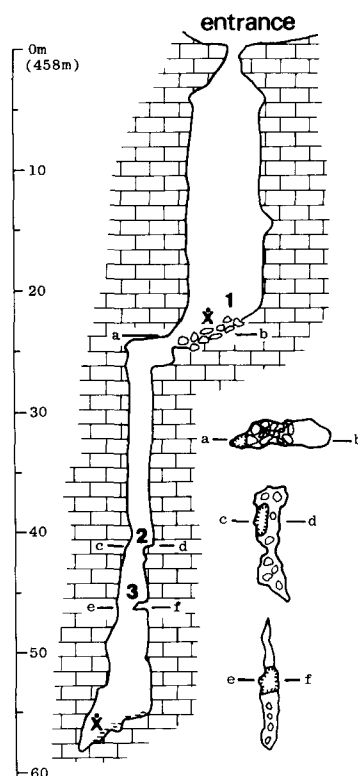


Fig. 57. Section (left figure) and plan (right lower figures) of Ohera-ana Cave. Redrawn from the figure by the Kitakyushu Caving Club. The scale on the left side indicates the depth of the cave (entrance=458 m above sea level).

1-3, number of terrace; X fossil site.

Ohera-ana Cave, Ninjinkubo First Cave, Yakubono-ana Cave, Ojika-do Cave (Chambers 1 and 2, and Branch 1), Oiwa-ana Cave and Yoshigatani Third Cave, whose geological settings are described below.

Hirao-ana Cave —

This cave opens on the southern slope of Mt. Ohera (587 m in elevation) which is situated on the northern edge of the Hirao-dai Plateau (Fig. 36). In December 1970, it was discovered by the members of the Kitakyushu Caving Club, and then explored by them.

This cave is a deep vertical pit with a depth of 68 m* (Fig. 56), and is formed along a joint

* MIZUSHIMA *et al.* (1982) recently measured it as 62 m.

striking N60°W to N70°W. Inside the cave, there are eight terraces with different levels. The upper surfaces of these terraces are covered by fallen blocks and reddish brown mud with breccia. In addition to these, black soil which seems to flow down from the entrance is also observed on the second terrace. The sediments on the second, fourth and sixth terraces contain mammalian remains. In the present study, the remains from the second terrace are exclusively examined, because they are much more abundant than those in other terraces.

Ohera-ana Cave —

This cave is situated only about 400 m east of Hirao-ana Cave (Fig. 36). It was also discovered and explored by the members of the Kitakyushu Caving Club in 1970. It is a deep vertical cave with a depth of about 60 m, which was formed along joints of limestone bedrock. Three terraces are observed between the entrance and bottom (1–3 in Fig. 57). Of these, the first terrace is widest. The floor of this terrace is covered by fallen blocks and black soil with breccia which contains mammalian remains. The bottom of the cave is about 34 m below the first terrace. Fallen blocks and reddish brown mud are deposited on its floor. This mud also yields mammalian remains. In the present study, the mammalian assemblage of the first terrace is examined.

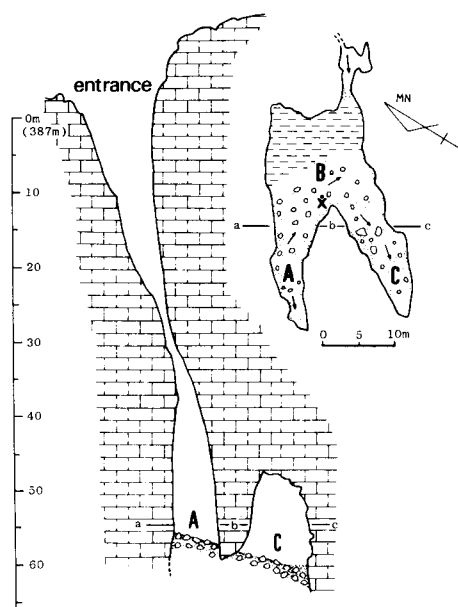


Fig. 58. Section (left) and plan (right) of Ninjin-kubo First Cave. Redrawn from the figure by the Exploration Club of Gakushuin University. The scale on the left side indicates the depth of the cave (entrance = 387 m above sea level).
X fossil site.

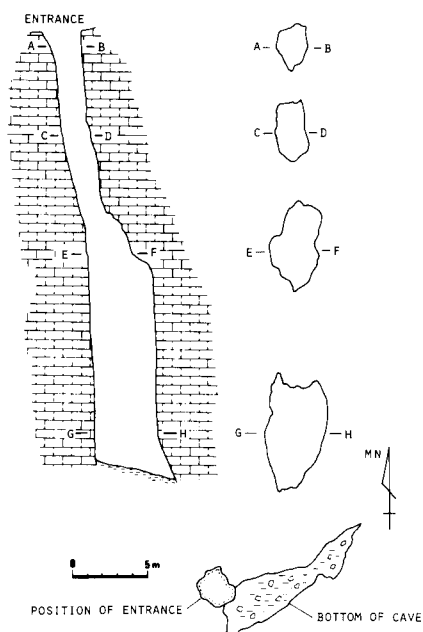


Fig. 59. Plan and section of Yakubono-ana Cave (plan = right-hand; section = left-hand). Redrawn from the figure by the Circle of Cave Study, Yamaguchi University.

Ninjinkubo First Cave —

This cave is situated at the north of Hirao, the only village on the plateau (Fig. 36). It is a deep vertical cave with a depth of 60 m (Fig. 58). It shows a fissure-like appearance, because it is formed along a joint striking N57°E and dipping 80°SE. No terraces are present between the entrance and bottom. The bottom has a V-shaped plan, and slopes down from A to C. Fallen blocks, breccia, mud and sand are deposited on its floor. These sediments yield abundant vertebrate remains at B. These remains are examined in the present study.

Yakubono-ana Cave —

This cave is situated about 400 m southeast of Ninjinkubo First Cave (Fig. 36). It is a vertical pit with a depth of 30 m (Fig. 59). The entrance has a round outline with a diameter of 3 m. There are no terraces between the entrance and bottom. The bottom is inclined north-eastward and covered by fallen blocks and black earth. The mammalian remains examined here were collected from this earth.

Ojika-do Cave —

This cave is one of the largest caves in the Hirao-dai Plateau, and is situated on the southern outskirts of Hirao (Fig. 36). According to MIZUSHIMA *et al.* (1982), it is 403 m in maximum length and 39 m in maximum depth. The structure of the cave is complicated by the combination of vertical and horizontal caves. Because the mammalian remains examined here are obtained from the area near the entrance, this area is exclusively described below. In the following description, the names of chamber and branch by HASEGAWA *et al.* (1968) are used.

From the entrance, a large vertical pit with a depth of about 25 m leads us to Chamber 1 (Fig. 60). This chamber shows a L-shaped plan. Fallen blocks, and brecciated mud and

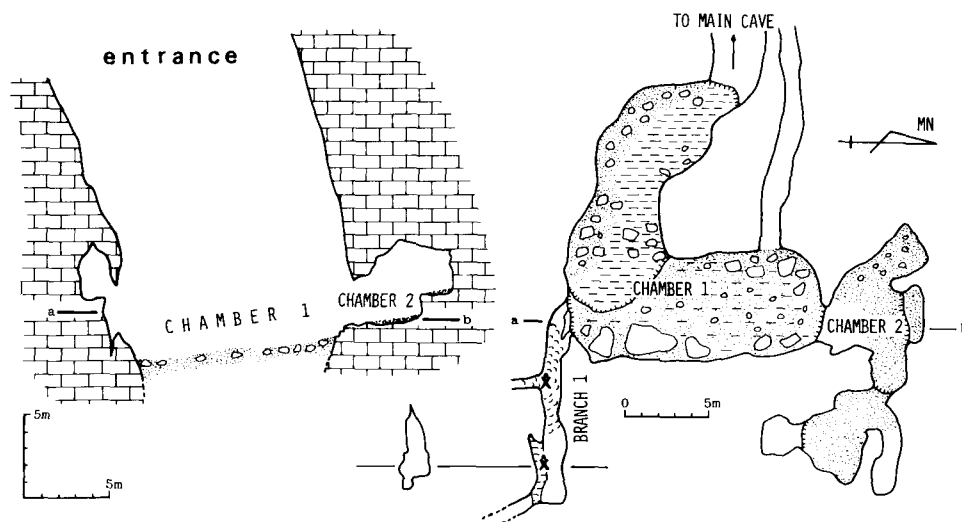


Fig. 60. Section (left) and plan (right) of Ojika-do Cave. Redrawn from the figure by the Exploration Club of Kokura Prison. The area near the entrance is exclusively shown. X fossil site in Branch 1. Mammalian remains are also obtained from Chambers 1 and 2.

sand are deposited on its floor. Chamber 1 is adjoined to a small hall (Chamber 2) at its northern end. The floor of Chamber 2 is covered by fallen blocks and sandy mud. A narrow tunnel called Branch 1 extends eastward from the south-eastern corner of Chamber 1. Its floor is partly covered by travertine or brecciated mud.

The mammalian remains are found in the muddy sediments of Chambers 1 and 2, and Branch 1. HASEGAWA *et al.* (1968) already reported the remains from these two chambers, but new materials were obtained after their investigation. These new materials are examined in the present study, although they are few in number.

Oiwa-ana Cave —

This cave is situated only 150 m southeast of Ojika-do Cave (Fig. 36). It is a vertical cave with a maximum depth of 22 m. The main part of the cave is cylindrical, and has no terraces between the entrance and bottom (Fig. 61). The bottom (A) inclines westward, and is connected with the floor of a narrow tunnel (B). This tunnel is only 1 m wide and extends south-westward.

The mammalian remains are found in reddish brown mud (partly mixed with humus) which is deposited on a notch formed on the wall of the main part 1 m above the bottom. These remains are examined in the present paper.

Yoshigatani Third Cave —

This cave opens on the eastern edge of the plateau near Mejiro-do Cave (Fig. 36). It is formed along a joint of crystalline limestone which strikes NS to N15°W and dips 63° to 66°W. A small terrace with an area of about 10 m² is found about 2 m below the entrance (Fig. 62). Its floor is covered by fallen blocks and black soil. About 8 m below this terrace, there is a slender hall with U-shaped plan. This hall covers an area of about 40 m². Brecciated mud and fallen blocks are deposited on its floor. The mammalian remains from this mud are examined in the present study. These remains are somewhat more fossilized than those from the above-mentioned six caves on Hirao-dai, but slightly less fossilized than those from

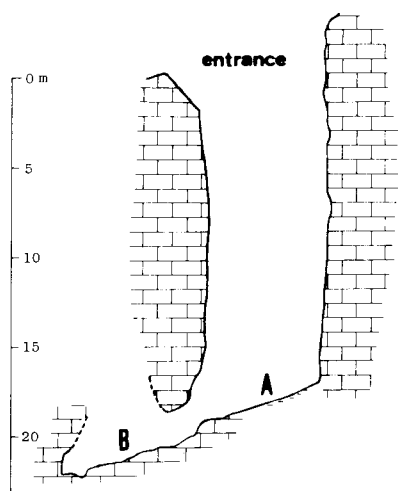


Fig. 61. Section of Oiwa-ana Cave. Redrawn from the figure by the Circle of Cave Study, Yamaguchi University. The scale on the left side indicates the depth of the cave.

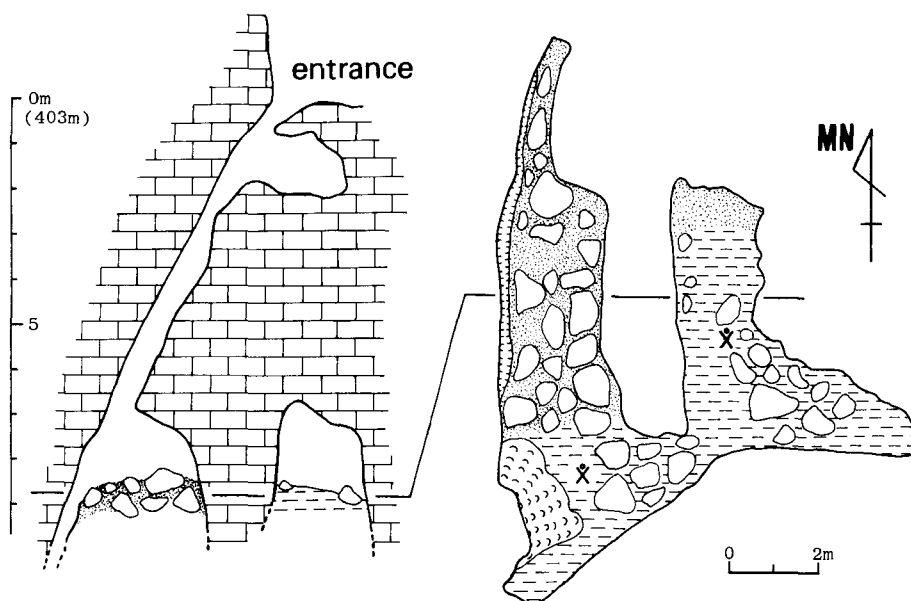


Fig. 62. Section (left) and plan (right) of Yoshigatani Third Cave. Redrawn from the figure by the Kitakyushu Caving Club. The scale on the left side indicates the depth of the cave (entrance=403 m above sea level). X fossil site.

Seiryukutsu Cave.

Paying attention to the occurrence of “*Sus nipponicus*” reported by SOTSUKA *et al.* (1982), KAWAMURA and SOTSUKA (1984) inferred that the fossiliferous sediments of this cave were Latest Pleistocene to Early Holocene in age. However the present author considers that the identification of the material from this cave with “*S. nipponicus*” is doubtful. Moreover, as pointed out by HAYASHI (1983), this species is possibly invalid and synonymized with *S. scrofa leucomystax*. Because no data positively indicate that the sediments of this cave are Late Pleistocene in age, they are regarded as Holocene in the present paper.

V. Fauna of Each Locality

A. Middle Pleistocene localities

The mammalian faunas of Ikumo Quarry, Sumitomo Quarry, and Localities 1, 3 and 4 of Ube Kosan Quarry are described here. As already mentioned in Chapter IV, the sediments of Site 3 of Yage Quarry are considered to be of Middle Pleistocene age. However the mammalian fauna of this site lacks rodents, and is composed of *Rhinolophus ferrumequinum* only (Table 7). Therefore, there is no need to give further descriptions to this fauna.

Table 4. Mammalian faunas of Ikumo Quarry, and Localities 1 and 4 of Ube Kosan Quarry. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth is shown. Black circle (●) indicates the occurrence known from other parts. Cross (+) shows the occurrence recorded by HASEGAWA (1963, 1966), although his identification is partly emended from the viewpoint of the present author.

LOCALITY AND LAYER TAXON		Ikumo Quarry	Locality 1 of Ube Kosan Quarry						Locality 4 of Ube Kosan Quarry
			Layer 1	Layer 2	Layer 3a	Layer 3b	Layer 4a	Layer 4b	
INSECTIVORA									
①Erinaceus Sp.	3	—	—	—	—	—	—	—	
*Sorex shinto	1	—	7	—	—	—	—	—	
Crociodura dsinezumi	1	1	13	—	1	—	—	—	
**Anourosorex japonicus	3	13	124	—	13	1	2	58	
*Dymecodon pilirostris	●	1	3	—	1	—	—	2	
*Dymecodon sp.	+	—	—	—	—	—	—	—	
Urotrichus talpoides	5	1	16	—	1	—	—	—	
Euroscaptor mizura	●	—	1	—	—	—	—	—	
Mogera wogura	+	—	—	—	—	—	—	—	
Mogera sp. A (small form)	1	2	9	—	4	—	1	4	
Mogera sp. B (large form)	—	—	—	—	1?	—	—	—	
CHIROPTERA									
Rhinolophus ferrumequinum	1	—	—	—	—	—	—	—	
Myotis Sp.	●	—	2	—	—	—	—	—	
Murina leucogaster	—	—	3	—	—	—	—	—	
Murina Sp. A	+	—	—	—	—	—	—	—	
Murina Sp. B	+	—	—	—	—	—	—	—	
LAGOMORPHA									
Lepus brachyurus	—	—	11	—	1	—	5	—	
**Lepus sp.	12	—	—	—	—	—	—	—	
RODENTIA									
Sciurus lis	+	—	—	—	—	—	—	—	
①Myopus schisticolor	+	—	—	—	—	—	—	—	
**Clethrionomys japonicus	6	13	78	1	16	—	1	20	
Microtus montebelli	—	1	4	—	—	—	—	—	
**Microtus epiratticepoides	+	1	10	—	2	—	2	1	
**Microtus cf. brandtioides	+	—	—	—	—	—	—	—	
Microtus sp. indet.	3	5	18	1	9	—	5	1	
Apodemus speciosus	2	5	17	2	10	—	1	103	
Apodemus argenteus	3	1	14	—	3	—	—	465	
Rattus aff. norvegicus	—	—	—	—	—	—	—	27	
Rattus sp.	+	—	—	—	—	—	—	—	
Glirulus japonicus	+	—	—	—	—	—	—	—	
CARNIVORA									
①Canis lupus	●	—	—	—	—	—	—	—	
Nyctereutes procyonoides	—	—	1	—	—	—	—	—	
*Ursus Sp.	+	—	—	—	—	—	—	—	
*Mustela erminea	+	—	—	—	—	—	—	—	
Mustela sibirica	1	—	1	—	—	—	—	—	
**Mustela constricta	+	—	—	—	—	—	—	—	
Meles moles anakuma	—	—	1	—	—	—	—	—	
**Meles leucurus kuzuensis	1	—	—	—	—	—	—	—	
**Meles mukasianakuma	+	—	—	—	—	—	—	—	
Martes sp.	1	—	—	—	—	—	—	—	
①Felis caracal	+	—	—	—	—	—	—	—	
PERISSODACTYLA									
**Rhinoceros sinensis	+	—	—	—	—	—	—	—	
ARTIODACTYLA									
Sus scrofa	—	—	—	—	—	—	1	—	
①Moschus Sp.	●	—	—	—	—	—	—	—	
**Sinomegaceros yabei	+	—	—	—	—	—	—	—	
**Cervus praenipponicus	+	—	—	—	—	—	—	—	
Cervus sp. indet.	●	1	2	—	2	—	1	—	

* exotic form to west Honshu; ① exotic form to Japan; ** extinct form.

1. Ikumo Quarry

21 forms of mammals are recognized in the OKAMURA Collection (Table 4). In addition to these, the previous authors reported the occurrence of 17 forms or more from this quarry (HASEGAWA, 1963, 1966; KOWALSKI and HASEGAWA, 1976; RZEBIK-KOWALSKA and HASEGAWA, 1976). Of these mammals, 11 forms are possibly extinct, while 5 forms are possibly exotic to the present Japanese Islands.

Rodent fauna —

Although the rodents are few in the OKAMURA Collection, KOWALSKI and HASEGAWA (1976) described eight forms on the basis of more materials. Of these forms, "*Clethrionomys rufocanus*" and "*Sciurus vulgaris*" are regarded as *C. japonicus*, sp. nov. and *Sciurus lis* in the present paper respectively. Moreover the materials identified as "*Microtus epiratticeps*" are divided into *M. epiratticepoides*, sp. nov. and *M. cf. brandtioides* here. The data provided by KOWALSKI and HASEGAWA (Table 19 of these authors) indicate that *C. japonicus* is most abundant, and *M. epiratticepoides* (including *M. cf. brandtioides*) is next in abundance. These arvicolid species are considered to be extinct species. An exotic arvicolid, *Myopus schisticolor* is few in abundance. This species is an inhabitant of taiga forests, so that its occurrence is indicative of colder climate than in the present day. The data of those authors also show that two murid species such as *Apodemus speciosus* and *A. argenteus* are relatively few, and moreover the remaining forms (*Sciurus lis*, *Rattus* sp. and *Glirulus japonicus*) are quite rare. In the assemblage of this locality, however, extant arvicolid species such as *Phaulomys smithii*, *P. andersoni* and *Microtus montebelli* are completely absent.

Associated fauna —

The insectivores are composed of ten forms. However *Dymecodon* sp. and *Mogera wogura* recorded by HASEGAWA (1963, 1966) might be equivalent to *D. pilirostris* and *Mogera* sp. A of the present author. *Erinaceus* sp. is an exotic form to the Japanese Islands. The remains of *Erinaceus* are unknown from other fossil localities in Japan. *Anourosorex japonicus* is an extinct species which is commonly found in the Middle and Late Pleistocene fossil localities.

In the present Honshu, Shikoku and Kyushu, some insectivores (*Sorex shinto*, *Dymecodon pilirostris* and *Euroscaptor mizura*) are restricted to high mountains, while others (*Crocidura dsinezumi*, *Urotrichus talpoides*, *Mogera wogura* and *M. kobeae*) are widely distributed in lowlands. Therefore in this paper, the former and latter are called "high mountain" and "lowland" forms respectively. In the present assemblage, both forms are found.

The chiropterans are rare in the OKAMURA Collection. Only two forms are present. In addition to these, HASEGAWA (1963, 1966) recorded two forms of *Murina*. At any rate, the chiropteran fauna of this quarry is quite insufficiently studied.

The lagomorph remains are abundant in the OKAMURA Collection. However they are assigned to a single form, *Lepus* sp. This form seems to be somewhat different from the extant species, *L. brachyurus*, which is widely distributed in the present Honshu, Shikoku and Kyushu.

The carnivores are rare in the OKAMURA Collection (only four forms), but the occurrence of other five forms is recorded by HASEGAWA (1963, 1966). The carnivore fauna of this quarry is

characterized by the predominance of extinct and exotic forms. Four of these forms are common to the fauna of the Upper Kuzuï Formation (*Canis lupus*, *Mustela erminea*, *Meles leucurus kuzuensis* and *M. mukasianakuma*), while *Mustela constricta* and *Felis caracal* are restricted to this quarry in Japan.

The perissodactyls are absent in the OKAMURA Collection, but HASEGAWA (1966) reported the occurrence of *Rhinoceros sinensis*. Its occurrence is important from biostratigraphic viewpoints, as stated in Chapter III (p. 44).

The artiodactyls are composed of two forms of cervids in the OKAMURA Collection. These forms are easily distinguishable from each other by size difference. The larger and smaller forms are assigned to *Cervus* and *Moschus* respectively. Additionally, HASEGAWA (1963, 1966) listed two extinct species such as *Sinomegaceros yabei* and *Cervus praenipponicus*.

General remarks —

The fauna of this quarry is characterized by the frequent occurrence of extinct forms and exotic forms to Japan. The ratio of these forms is estimated to be about 43% in all taxa as well as in other orders than rodents. This value approximates to those in Ando Quarry (43% in all taxa and 39% in other orders than rodents) which are calculated from the data provided by HASEGAWA (1966) and KOWALSKI and HASEGAWA (1976). On the other hand, the ratio in the present fauna is lower than that in Sumitomo Quarry, but higher than those in Localities 1 and 3 of Ube Kosan Quarry. It is assumed that these differences are related to those in geological age among the localities.

From an ecological viewpoint, the present fauna is characterized by the predominance of woodland elements. Moreover several elements indicate cooler climate than in the present day. Therefore it is assumed that forests of the cooler temperate zone were developed around this quarry, when the fossiliferous sediments were deposited.

2. Sumitomo Quarry

The following mammals are known from the fossiliferous sediments of this quarry:

Order Insectivora

1. *Sorex shinto* THOMAS

Order Chiroptera

2. *Pleistomyotis longihumeralis* KURAMOTO et YOON
3. *Myotis okafujii* KURAMOTO et YOON
4. *Myotis beppuensis* KURAMOTO et YOON
5. *Miniopterus schreibersii* (KÜHL)

Order Rodentia

6. *Cricetulus* sp.
7. *Clethrionomys japonicus*, sp. nov.
8. *Apodemus speciosus* (TEMMINCK)

Order Carnivora

9. *Vulpes vulpes japonica* GRAY
10. ?*Selenarctos thibetanus* (CUVIER)
11. *Felis* sp.

1 was newly discovered by the present author, while 2 to 5, 6, 8 and 9 to 11 are cited from YOON *et al.* (1984), KAWAMURA (1977b), KOWALSKI and HASEGAWA (1976) and HASEGAWA

(1980b). 7 was originally assigned to "*Clethrionomys rufocanus*" by KOWALSKI and HASEGAWA (1976), but is emended in the present paper.

Of these 11 forms, 2, 3, 4 and 7 are extinct species, while 6 and 11 are exotic forms to the Japanese mainland.

Rodent fauna —

The rodents are extremely rare in number, but assigned to three forms. Of these, *Cricetulus* sp. is most important, because the occurrence of this genus is confined to this quarry in Japan, and is indicative of arid environments. The remaining two species are commonly found in other Middle Pleistocene localities of Japan.

Associated fauna —

The insectivores and carnivores are very uncommon, but referred to the above-listed four forms. On the other hand, the chiropterans are highly predominant in the present fossil assemblage. Moreover almost all the fossils are assigned to only two extinct species, *Myotis okafujii* and *M. beppuensis*. These species are unknown from other fossil localities. The remaining two species are extremely rare. Of these, an extinct species, *Pleistomyotis longihumeralis* is also confined to this locality.

General remarks —

As mentioned above, the present fauna is characterized by the extremely high proportion of the two species of bats. This possibly indicates that the present assemblage was originated from dense colonies of these bats in a cave.

In the present fauna, the ratio of extinct forms plus exotic forms to Japan attains to 54.5% in all taxa, and 50.0% in other orders than rodents. These values are highest in the Quaternary fossil localities of Japan which yield micro-mammals as well as middle- or large-sized mammals.

Although *Cricetulus* mainly occurs in the steppe zone of the present Palaearctic Region, a few elements of the present fauna are considered to be inhabitants of temperate forests. Therefore the fauna suggests open woodlands or woody grasslands under drier climate than in the present day.

3. Locality 1 of Ube Kosan Quarry

The abundance of fossil mammals obtained from each layer is shown in Table 4. The fossils are rich in Layers 1, 2 and 3b, but poor in Layers 3a, 4a and 4b. Because the faunal compositions are not fundamentally different in each layer, they can be treated altogether. As a whole, the fauna of this locality comprises 21 forms of mammals including three extinct species (excluding *Microtus* sp. indet.).

Rodent fauna —

Clethrionomys japonicus is most abundant, and its number far exceeds the total of *Microtus* remains. The genus *Microtus* is composed of a living species, *M. montebelli*, and an extinct species, *M. epiratticepoides*. The latter is much more than the former. The murids are less than the arvicolids, and comprise two extant species, *Apodemus speciosus* and *A. argenteus*. The abundance of the former is nearly equal to that of the latter.

Associated fauna —

The insectivores are composed of eight forms. Of these, *Anourosorex japonicus* is highly predominant, and exceeds the total of the remaining forms in number. The lowland forms are much more than the high-mountain forms.

The chiropterans comprise only two forms, which are poor in number. The lagomorph remains are assigned to a single living species, *Lepus brachyurus*. The carnivores are also poor in variety (only three species) and in number.

The artiodactyls are composed of *Sus scrofa* and *Cervus* sp. indet. The former is represented by a single fragmental molar which is well coincident with the living *S. scrofa* in morphology and size. *Sus* is never found in the faunas of other Middle Pleistocene localities described here. The remains of *Cervus* are assignable to a single species, but their specific determination is impossible because of the lack of well-preserved antlers.

General Remarks —

The ratio of extinct forms plus exotic forms to Japan is much lower than that in Ikumo Quarry. On the other hand, the faunal composition suggests the sylvan environments which are similar to those in west Honshu of the present day.

4. Locality 3 of Ube Kosan Quarry

The mammalian fauna of this locality comprises at least 33 forms (Fig. 63 and Table 5). Of these, seven forms are extinct, while no exotic forms to Japan are found. Observed in detail, the faunas of the lower layers are somewhat different from those of the upper layers (Fig. 63). Such a difference is most remarkable in arvicolids as mentioned below.

Rodent fauna —

Arvicolids and murids are abundant, while sciurids are very rare and glirids are absent. The arvicolids comprise four forms including three extinct forms. Of these, *Clethrionomys japonicus* is abundant in the lowest layers (Layers 1 to 4), but somewhat decreases in Layers 5 to 10. In Layers 11 to 14, it is further diminished. On the contrary, it somewhat increases in the uppermost layers (Layers 15 to 18). The genus *Microtus* comprises the remaining three forms. Of these, *M. montebelli* and *M. epiratticepoides* are abundant, while *M. cf. brandtioides* is very rare. In the lower layers, *M. montebelli* is considerably surpassed by *M. epiratticepoides* in number. In the upper layers, however, the former species remarkably increases and exceeds the latter in number.

The murids are composed of *Apodemus speciosus* and *A. argenteus* only. The frequency of *A. speciosus* approximates to that of *A. argenteus* in the lower layers, while the former becomes much lower than the latter in the upper layers.

Associated fauna —

The insectivores are composed of eight forms. Of these, *Crociodura dsinezumi*, *Anourosorex japonicus* and *Urotrichus talpoides* are dominant, while *Mogera* sp. A is subordinate. The remaining four forms are rarely found. When these insectivores are divided into the lowland and high-mountain forms, the former is much more abundant than the latter.

The chiropterans are considerably fewer than the insectivores, but comprise seven forms.

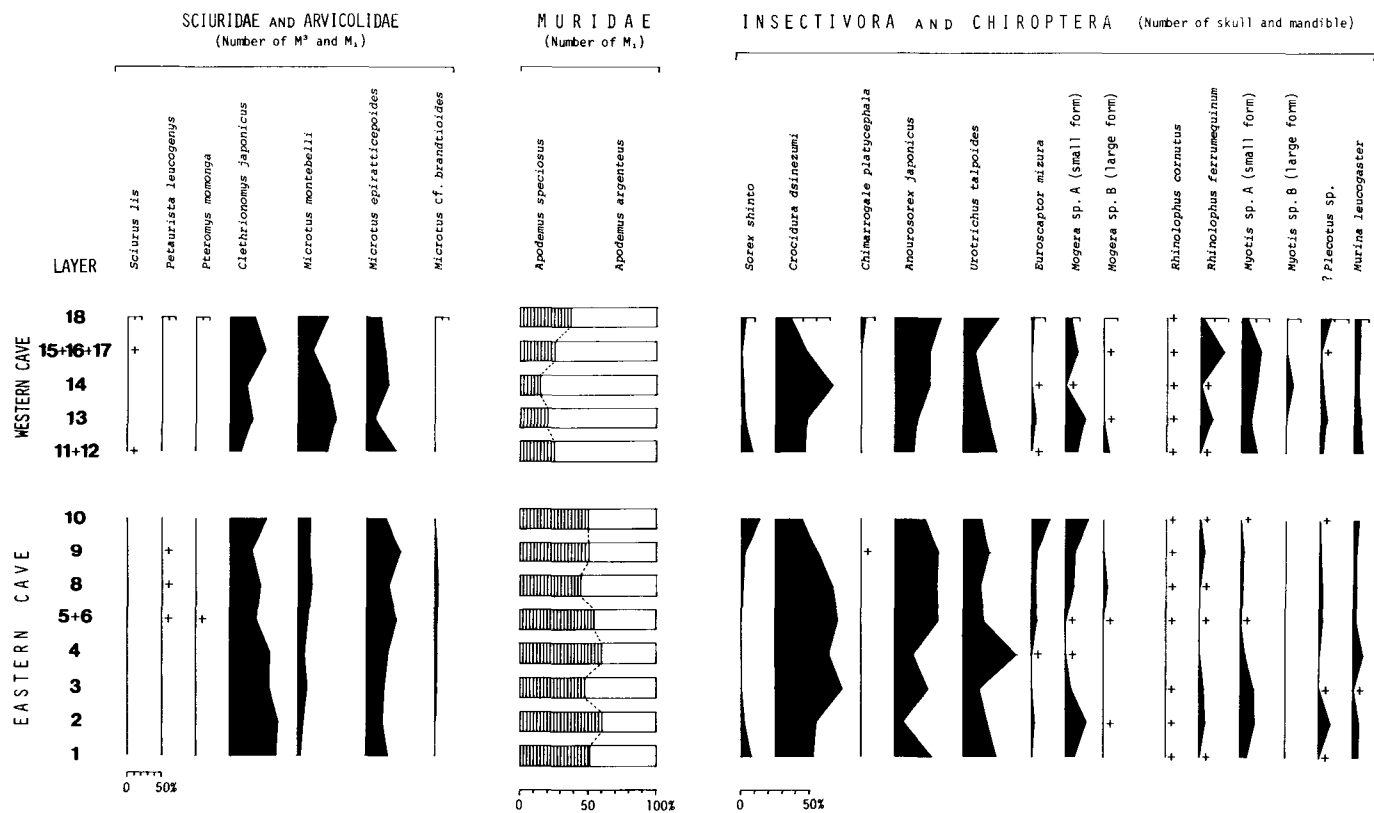


Fig. 63. Diagram showing the relative abundance of micro-mammals in each layer of Locality 3 of Ube Kosan Quarry. The abundance is calculated by the number of M^3 and M_1 in sciurids and arvicolids, by the number of M_1 in murids and by the number of skull and mandible in insectivores and chiropterans. Cross (+) indicates the occurrence known from other bones and teeth than these parts.

Table 5. Stratigraphic distribution of the fossils of primates, lagomorphs, carnivores and artiodactyls in Locality 3 of Ube Kosan Quarry. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth is shown in each layer.

LAYER \ TAXON		PRIMATES	<i>Macaca fuscata</i>	LAGOMORPHA	<i>Lepus brachyurus</i>	CARNIVORA	<i>Nyctereutes procyonoides</i>	* <i>Mustela erminea</i>	<i>Mustela sibirica</i>	** <i>Mustela kuzuensis</i>	** <i>Mustela</i> sp.	<i>Meles meles anakuma</i>	** <i>Meles leucurus kuzuensis</i>	ARTIODACTYLA	** <i>Cervus praenipponicus</i>	<i>Cervus</i> sp. indet.
WESTERN CAVE	horizon unknown	—	—	5	—	—	—	—	1	—	1	1	—	—	3	—
	18	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—
	17	—	—	5	—	—	—	—	—	—	—	1	—	—	1	—
	16	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
	14	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—
	13	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—
	12	1	—	—	—	—	—	—	1	—	1	—	—	—	—	—
	11	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
	9	—	—	2	—	2	1	—	1	—	—	—	—	—	—	1
	8	—	—	1	1	—	1	1	—	1	1	—	—	—	—	1
	6	1	—	2	—	2	5	1	—	10	2	—	—	—	—	2
	4	1	20	—	—	1	1	1	8	3	—	—	—	—	1	23
	3	—	—	—	—	—	—	—	—	—	12	—	—	—	—	—
	2	—	—	1	—	—	1	—	—	—	1	—	—	—	—	—
	1	—	—	4	—	1	1	—	—	—	2	—	—	—	—	—

* exotic form to west Honshu; ** extinct form.

Of these, *Rhinolophus ferrumequinum*, *Myotis* sp. A and *Murina leucogaster* are relatively abundant. The two forms of *Myotis* are specifically different from the extinct species known from Sumitomo Quarry.

The primates and lagomorphs are composed of a single extant species respectively. The carnivores comprise seven forms which include three extinct forms. Of these extinct species, *Mustela kuzuensis* and *Meles leucurus kuzuensis* are common elements to the fauna of the Upper

Kuzuï Formation. All the remains of artiodactyls are assigned to *Cervus*. Because a single antler from Layer 4 is identified as *C. praenipponicus*, other remains of *Cervus* from this layer might be referred to the same species. However the specific determination of the remains from other layers is reserved because of the lack of identifiable antlers.

General remarks —

The ratio of extinct forms plus exotic forms to Japan is estimated to be about 24% in all taxa and about 21% in other orders than rodents. These values are considerably lower than those in Ikumo Quarry and Sumitomo Quarry, but generally come near to those in the Late Pleistocene localities. These facts are consistent with the results of the U-series dating, amino-acid dating and fluorine test.

The composition of the present fauna is generally similar to that of Locality 1 of the same quarry. Especially the fauna of Layers 1 to 4 of the present locality strongly resembles that of Locality 1 in the following points:

1. *Clethrionomys* is more abundant than *Microtus*.
2. *Microtus epiratticepoides* is more abundant than *M. montebelli*.
3. The frequency of *Apodemus argenteus* approximates to that of *A. speciosus*.

From the ecological viewpoint, the present fauna is regarded as a temperate forest type, and suggests the similar climatic and vegetational conditions to those in the present day.

5. Locality 4 of Ube Kosan Quarry

The mammals obtained from this locality are restricted to Rodentia and Insectivora (Table 4). They are assigned to eight forms (excluding *Microtus* sp. indet.) which include three extinct species.

Rodent fauna —

The murids are much more abundant than the arvicolids. This fact depends partly on the poor preservation of the arvicolid remains in the present fossil assemblage, but mainly reflects the relative abundance of the original population. In the murids, *Apodemus argenteus* is highly predominant. This species is restricted to woodlands in the present Japan. *A. speciosus* is next in abundance, which far exceeds *Rattus* aff. *norvegicus* in number. In the arvicolids, *Clethrionomys japonicus* is more abundant than *Microtus* which is represented by a single specimen of *M. epiratticepoides*. These two species are extinct, while the living arvicolids such as the species of *Phaulomys* and *Microtus montebelli* are absent from the present assemblage.

Associated fauna —

The insectivores are much poorer than the rodents in number, but comprise three forms (Table 4). Of these three, *Anourosorex japonicus* is highly predominant. However the remaining two are rare.

General remarks —

The mammalian fauna of this locality is similar to that of Locality 1 of the same quarry in the following points:

1. The components of the former fauna are mostly common to those of the latter (*Rattus* is the only exception).
2. *Anourosorex japonicus* is highly predominant in the insectivore assemblage.

3. *Clethrionomys* is more abundant than *Microtus*.

The faunal composition strongly suggests sylvan environments of the temperate zone as in the present day.

B. Late Pleistocene localities

1. Aisawa Quarry

Twelve forms of mammals are recognized in the present assemblage (excluding *Microtus* sp. indet.). They include only one extinct form (*Meles leucurus kuzuensis*). The abundance of each form is shown in Table 6.

Rodent fauna —

The rodents are fairly poor in variety. Namely only two genera such as *Microtus* and *Apodemus* are recognized. The former is more abundant than the latter. The remains of *Microtus* which are identifiable in specific level are exclusively assigned to *M. montebelli*. On the other hand, the remains of *Apodemus* are assigned to two species such as *A. speciosus* and *A. argenteus*. The former species is more abundant than the latter.

Associated fauna —

The insectivores comprise four forms which are extant or near to extant species. Three of these four are referred to lowland forms, which are highly predominant in abundance.

The chiropterans and carnivores are poor in variety and number. These orders comprise two forms each. The remains of artiodactyls are assigned to a single form of *Cervus*. However its specific determination is impossible because of the lack of identifiable antlers. *Sus* is never found in the present assemblage.

General remarks —

The fauna of this locality is generally coincident with the lowland fauna of central Honshu in the present day. Therefore it is assumed that the area around this locality was covered by temperate forests, when the fossiliferous sediments were deposited. However the abundant occurrence of *Microtus* possibly suggests that the forests were considerably open and showed a parkland-like aspect.

2. Nojiri-ko Formation

THE EDITORIAL COMMITTEE OF MONOGRAPH NO. 27 OF THE ASSOCIATION FOR THE GEOLOGICAL COLLABORATION IN JAPAN (1984) provided the stratigraphic distribution of the following five mammals which were known from the Nojiri-ko Formation:

<i>Microtus</i> sp.	Section I of Upper Member.
<i>Ursus arctos</i> LINNAEUS	Section II of Middle Member.
<i>Palaeoloxodon naumanni</i> (MAKIYAMA)	Section III of Lower Member to Section I of Upper Member.
<i>Cervus nippon</i> TEMMINCK	Section III of Lower Member.
<i>Sinomegaceros yabei</i> (SHIKAMA)	Section III of Lower Member to Section I of Upper Member.

It is assumed that the fossil assemblage was formed mainly by the hunting activities of the Palaeolithic men.

Table 6. Mammalian faunas of Aisawa Quarry, Suse Quarry, Locality 2 of Ube Kosan Quarry and Husen-ana Cave. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth is shown. Additionally black circle (●) indicates the occurrence known from other parts.

TAXON	LOCALITY			LATE PLEISTOCENE		HOLOCENE	
	Aisawa Quarry	East Fissure of Suse Quarry	Loc.2 of Ube Kosan Quarry	West Fissure of Suse Quarry	Husen-ana Cave		
INSECTIVORA							
<i>Crocidura dsinezumi</i>	9	1	—	—	10		
<i>Urotrichus talpoides</i>	14	14	1	4	5		
<i>Euroscaptor mizura</i>	1	—	—	—	—		
<i>Mogera</i> sp. A (small form)	13	2	—	●	3		
<i>Mogera</i> sp. B (large form)	—	4	—	●	14		
CHIROPTERA							
<i>Rhinolophus cornutus</i>	—	—	—	—	1		
<i>Rhinolophus ferrumequinum</i>	1	2	1	—	3		
<i>Myotis macrodactylus</i>	—	—	3	—	—		
<i>Myotis</i> sp.	1?	—	—	—	—		
<i>Murina leucogaster</i>	—	—	2	—	—		
PRIMATES							
<i>Macaca fuscata</i>	—	3	—	—	—		
LAGOMORPHA							
<i>Lepus brachyurus</i>	—	—	—	7	—		
RODENTIA							
<i>Petaurista leucogenys</i>	—	1	—	—	—		
<i>Clethrionomys-Phaulomys</i> group	—	—	1	—	—		
<i>Phaulomys</i> Cf. <i>smithii</i>	—	3	—	—	215		
<i>Microtus montebelli</i>	13	3	—	—	1		
** <i>Microtus epiratticepoides</i>	—	—	1	—	—		
<i>Microtus</i> sp. indet.	32	2	2	—	1		
<i>Apodemus speciosus</i>	10	10	6	31	65		
<i>Apodemus argenteus</i>	4	4	8	1	13		
CARNIVORA							
<i>Vulpes vulpes</i>	—	—	—	1	—		
<i>Nyctereutes procyonoides</i>	—	1	—	9	—		
<i>Martes melampus</i>	—	—	—	—	1		
<i>Mustela sibirica</i>	3	1	—	1	1		
<i>Meles meles</i>	—	—	—	8	1		
** <i>Meles leucurus kuzuuensis</i>	1	—	—	—	—		
ARTIODACTYLA							
<i>Sus scrofa</i>	—	—	—	5	—		
** <i>Cervus praenipponicus</i>	—	1	—	—	—		
<i>Cervus</i> sp. indet.	9	62	—	●	—		

** extinct form.

Rodent fauna —

The rodent remains are composed only of two molars and one incisor which are poorly preserved. The molars and incisor were assigned to *Microtus* sp. and *Myomorpha*, gen. et sp. indet. respectively (KAWAMURA and FOSSIL MAMMAL RESEARCH GROUP OF NOJIRI-KO EXCAVATION, 1979). However the morphological study of the incisors of the Japanese living myomorph rodents by the present author recently revealed that the incisor was possibly identifiable as *Microtus*.

Associated fauna —

The associated fauna comprises two extinct species (*Palaeoloxodon naumanni* and *Sinomegaceros yabei*), one exotic species to Honshu (*Ursus arctos*) and one extant species (*Cervus nippon*). The first two species are highly predominant in this assemblage, while others are rare. Such a strong bias possibly reflects biased games of hunting by the Palaeolithic men.

3. Sugi-ana Cave

The mammalian fossils obtained from this cave are assigned to 19 forms. Of these, 17 forms are shown in Figs. 64 and 65. The remaining two are *Macaca fuscata* and *Lepus brachyurus*. These 19 forms include three extinct forms (*Anourosorex japonicus*, *Microtus epiratticepoides* and *M. cf. brandtioides*) and one transitional form between living and fossil species (*Clethrionomys-Phaulomys* transitional form).

Rodent fauna —

The rodents are most abundant in the present fossil assemblage (Fig. 64), and comprise seven forms. Of these, *Clethrionomys-Phaulomys* transitional form is predominant (Fig. 65). *Microtus montebelli* is next in abundance, but is far surpassed by the transitional form. The two extinct forms of *Microtus* are considerably scarce. The murids are much fewer than these arvicolids. They consist of *Apodemus speciosus* and *A. argenteus*. The former species is somewhat more abundant than the latter. The glirid remains are extremely rare, which are exclusively referred to *Glirulus japonicus*.

Associated fauna —

The insectivores are composed of seven forms. Of these, *Dymecodon pilirostris* is most abundant, while *Urotrichus talpoides* is next in abundance. The remaining forms are relatively scarce. When these insectivores are divided into high-mountain and lowland forms, the former is more abundant than the latter.

The chiropterans are scarce in the present fossil assemblage. They are assignable to two extant forms and one form which is very near to the extant species. The primates and lagomorphs are rarely found, which are composed of a single species each.

General remarks —

The fauna of this locality is composed mainly of micro-mammals. The composition of taxa in specific level is similar to those in the faunas of the Middle Pleistocene localities such as Localities 1, 3 and 4 of Ube Kusan Quarry. However the present fauna is remarkably different from the faunas of these localities in the relative abundance of such extinct species as *Anourosorex japonicus* and *Microtus epiratticepoides*, and of such extant species as *Dymecodon pilirostris* and *M.*

montebelli. Namely the frequencies of the former species are much lower in the present fauna than in the localities of Ube Kosan Quarry, while those of the latter species show an inverse tendency.

The present fauna is also similar to that of F_3 of Kumaishi-do Cave in the composition of taxa. However the following differences are observed in the relative abundance of several

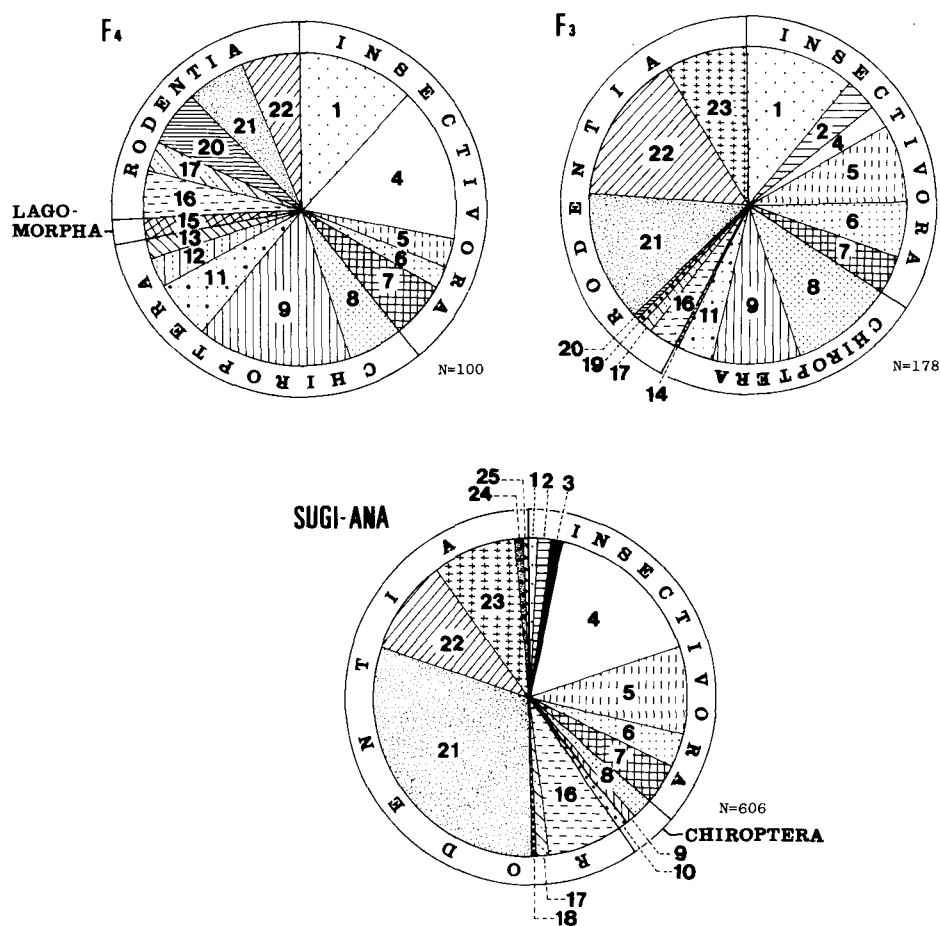


Fig. 64. Pie diagrams comparing the relative abundance of micro-mammals in F_4 and F_3 of Kumaishi-do Cave, and in Sugi-ana Cave. The ratio of the number of mandibles is shown. N, number of examined specimens.

Insectivora (1–7): 1, *Sorex shinto*; 2, *Crocidura dsinezumi*; 3, *Anurosorex japonicus*; 4, *Dymecodon pilirostris*; 5, *Urotrichus talpoides*; 6, *Euroscaptor mizura*; 7, *Mogera* sp.

Chiroptera (8–14): 8, *Rhinolophus cornutus*; 9, *R. ferrumequinum*; 10, *Myotis* cf. *macroclactylus*; 11, *Myotis* sp.; 12, *Miniopterus schreibersii*; 13, ? *Plecotus* sp.; 14, *Murina leucogaster*.

Lagomorpha: 15, *Lepus brachyurus*.

Rodentia (16–25): 16, *Clethrionomys-Phaulomys* transitional form; 17, *Microtus montebelli*; 18, *M. epiratticepoides*; 19, *M.* cf. *brandtoides*; 20, *M.* sp. indet.; 21, Arvicolidae, gen. et sp. indet.; 22, *Apodemus speciosus*; 23, *A. argenteus*; 24, Muridae, gen. et sp. indet.; 25, *Glirulus japonicus*.

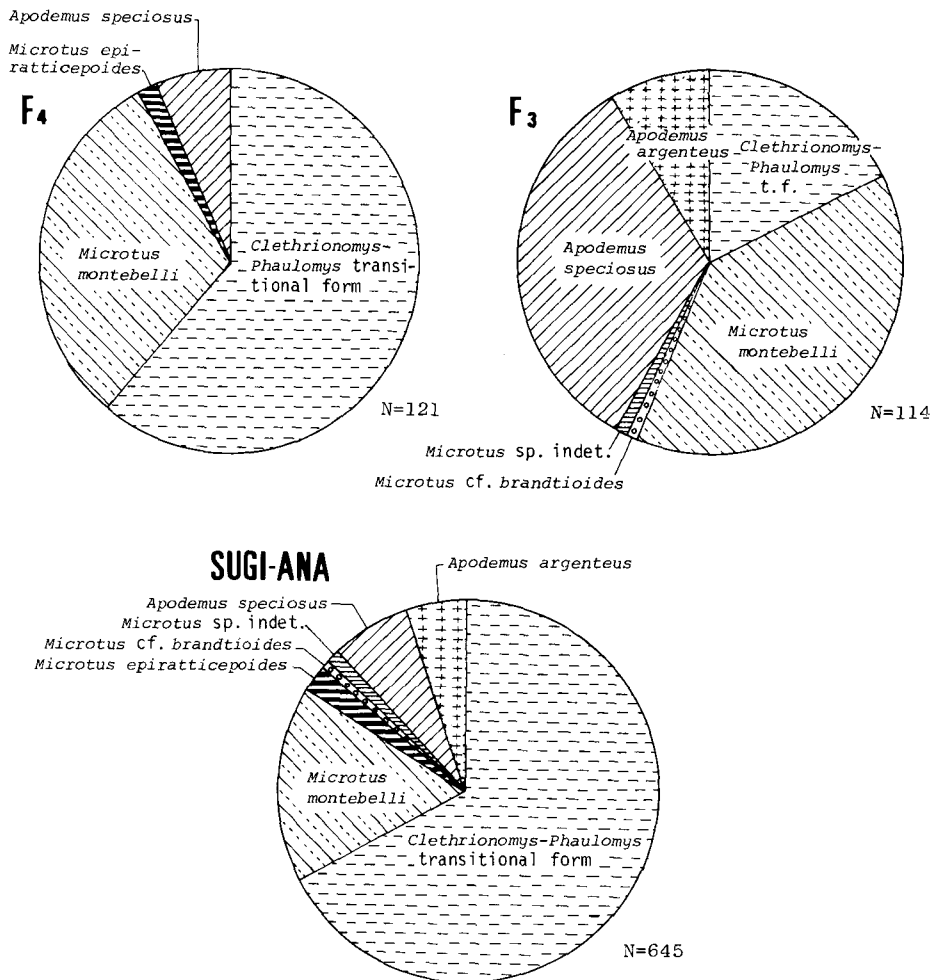


Fig. 65. Pie diagram comparing the relative abundance of rodents in F₄ and F₃ of Kumaishi-do Cave, and in Sugi-ana Cave. The ratio of the number of M₁ is shown. N, number of examined specimens.

forms (Figs. 64, 65):

1. In the present fauna, *Sorex shinto* is much fewer, but *Anourosorex japonicus* and *Dymecoeon pilirostris* are more abundant than in the fauna of F₃.
2. The chiropterans are less abundant in the present fauna.
3. In the present fauna, *Clethrionomys-Phaulomys* transitional form is more abundant, while *Microtus montebelli* and *Apodemus speciosus* are less abundant.
4. The extinct species of *Microtus* are more abundant in the present fauna.

The composition of micro-mammalian taxa in the present fauna is generally coincident with that in the fauna of F₄ of Kumaishi-do Cave. However the following differences are also recognized between these two faunas (Figs. 64, 65).

1. *Anourosorex japonicus* and *Crocidura dsinezumi* are existent in the present fauna, but absent from the

fauna of F₄.

2. *Sorex shinto* and *Microtus montebelli* are less abundant in the present fauna than in the fauna of F₄.

3. *Urotrichus talpoides* and *Apodemus argenteus* are more abundant in the present fauna.

These possibly reflect the differences in geological age and palaeoenvironments among these localities. From the ecological viewpoint, the composition of the fauna of Sugi-ana Cave suggests the temperate forests which were developed under somewhat cooler climate than in the present day.

4. F₄ of Kumaishi-do Cave (including F₁ and F₂)

28 forms of mammals are obtained from the fossiliferous sediments of F₄, F₁ and F₂. Of these, 18 forms are referred to micro-mammals. Figs. 64 and 65 show the relative abundance of the micro-mammals estimated from the number of mandibles and M₁. In these figures, however, the following three forms are not represented because of the lack of mandible and M₁:

Microtus cf. *brandtioides* YOUNG

Apodemus argenteus (TEMMINCK)

Glirulus japonicus (SCHINZ)

The middle- and large-sized mammals are assigned to the following 10 forms:

Macaca fuscata (BLYTH)

Nyctereutes procyonoides (GRAY)

Ursus sp.

Selenarctos thibetanus (CUVIER)

Mustela nivalis LINNAEUS

Meles meles (LINNAEUS)

Palaeoloxodon naumanni (MAKIYAMA)

Cervus praenipponicus SHIKAMA

Sinomegaceros yabei (SHIKAMA)

Alces alces (LINNAEUS)

The present fauna contains five extinct forms, one transitional form between living and fossil species, and one exotic form to the Japanese Islands.

Rodent fauna —

The rodent remains are assignable to seven forms which include two extinct forms such as *Microtus epiratticepoides* and *M.* cf. *brandtioides*. Of these seven, *Clethrionomys-Phaulomys* transitional form is most abundant, which is followed by *M. montebelli*, *Apodemus speciosus* and *M. epiratticepoides* in order of abundance. The remaining three forms (*M.* cf. *brandtioides*, *A. argenteus* and *Glirulus japonicus*) are very rare (one or two specimens each). The frequency of the above-mentioned extinct forms is lower than that in the assemblage of Sugi-ana Cave, but approximates that in F₃ of Kumaishi-do Cave.

Associated fauna —

The insectivore fauna is composed of five forms which include neither extinct form nor exotic form to Honshu. As regards the relative abundance of each form, *Sorex shinto* and *Dymecodon pilirostris* are predominant, while other three forms are much fewer than these. Therefore the frequency of high-mountain forms is much higher than that of lowland forms.

The chiropterans are considerably abundant in comparison with those in Sugi-ana Cave and F₃. They comprise five forms. Of these, *Rhinolophus ferrumequinum* is most abundant.

The remains of primates and lagomorphs are assigned to one species each (*Macaca fuscata* and *Lepus brachyurus*). The former species is extremely rare, while the latter is commonly found. The carnivore remains are relatively few in the present fauna, and are assigned to five forms. Excepting *Ursus* sp., all of them are living species which are now distributed in Honshu. On the other hand, *Ursus* sp. has a strong resemblance to *Ursus arctos* which is absent from the present Honshu.

Large herbivores such as proboscideans and artiodactyls are relatively abundant in the present assemblage. The proboscidean remains are assigned to a single extinct species, *Palaeoloxodon naumanni*, while the artiodactyl remains are referred to two extinct species (*Cervus praenipponicus* and *Sinomegaceros yabei*) and one exotic species to the Japanese Islands (*Alces alces*). Because the last species is widely distributed in taiga forests of the present Holarctic Region, its occurrence indicates cold climates.

General remarks —

The ratio of extinct forms plus exotic forms to Japan attains to 25% in all taxa and 19% in other orders than rodents. These values are generally higher than in other Late Pleistocene localities of Japan. This fact reflects the abundant occurrence of the extinct and exotic large herbivores in the present fauna.

The composition of the present fauna is indicative of woodland environments. The predominance of high-mountain forms in the insectivore fauna and the presence of *Alces alces* also suggest that the climate was considerably colder than in the present day, when the sediments of F₄ were deposited.

5. F₃ of Kumaishi-do Cave

The fauna of F₃ comprises 20 forms of mammals in which micro-mammals highly predominate (19 forms). Of these, the relative abundance of 16 forms calculated from the number of mandibles and M₁ is shown in Figs. 64 and 65. The remaining four forms are not represented in these figures, because their occurrences are known from other parts than mandible and M₁. They are listed as follows:

Anourosorex japonicus SHIKAMA et HASEGAWA

Microtus epiratticepoides, sp. nov.

Murina aurata MILNE-EDWARDS

Cervus sp.

Each of them is very scarce (one or two specimens only). In these 20 forms, there are three extinct forms and one transitional form between living and fossil species which also occur in the fauna of Sugi-ana Cave.

Rodent fauna —

The rodent fauna is composed mainly of *Microtus montebelli* and *Apodemus speciosus* which are followed by *Clethrionomys-Phaulomys* transitional form and *A. argenteus* in order of abundance (Fig. 65). On the other hand, two extinct forms, *M. epiratticepoides* and *M. cf. brandtioides*, are rarely found. Sciurids and glirids are absent.

Associated fauna —

The insectivores comprise seven forms which include one extinct species, *Anourosorex japonicus*, in very low frequency. Of these seven, *Sorex shinto* is most abundant, while *Urotrichus talpoides* is next in abundance (Fig. 64). The frequency of the high mountain forms approximates to that of lowland forms.

The chiropterans are abundant in comparison with those in the assemblage of Sugi-ana Cave. They are composed mainly of *Rhinolophus cornutus* and *R. ferrumequinum*. However *Myotis* sp. is less abundant than these, and moreover *Murina leucogaster* is very rare.

Middle- and large-sized mammals are scarcely found. Only one cheek tooth fragment is assigned to *Cervus* sp.

General remarks —

The present fauna is indicative of temperate forests which are presumably more open than the forests suggested by the fauna of Sugi-ana Cave. In the composition of micro-mammalian taxa, it is fairly similar to the fauna of F₄ of the same cave. However the following differences are also observed between these two faunas:

1. *Crocodyra dsinezumi* rarely occurs in F₃, but is absent from F₄.
2. On the contrary, *Miniopiterus scheibersii*, *Plecotus* sp. and *Lepus brachyurus* are absent from F₃, but occur in F₄.
3. *Dymecodon pilirostris*, *Rhinolophus ferrumequinum* and *Clethrionomys-Phaulomys* transitional form are less abundant in F₃ than in F₄.
4. *Urotrichus talpoides*, *R. cornutus*, *Microtus montebelli*, *Apodemus speciosus* and *A. argenteus* are more abundant in F₃ than in F₄.

These differences are partly resulted from the difference in climatic condition between these two faunas. Namely it is assumed that the sediments of F₃ were deposited under somewhat warmer climate than those of F₄.

6. Yage Quarry

The abundance of the mammalian remains collected from this quarry is shown in Table 7. The detailed description on the fauna of each site is given below, where Site 3 is excluded because of its earlier geological age (Middle Pleistocene).

Site 1 —

The mammalian remains examined in the present study are assigned to eight forms (excluding *Microtus* sp. indet.). In addition to these, TOMIDA (1978) recorded the following five species from the "Upper Yage Formation" of Fissure H, which is presumably equivalent to this site:

Mogera wogura (TEMMINCK)
Lepus brachyurus TEMMINCK
Nyctereutes procyonoides (GRAY)
Mustela sibirica PALLAS
Cervus praenipponicus SHIKAMA

These 13 forms include three extinct species (two species asterisked in Table 7 and *C. praenipponicus*).

The rodents are scarce in the examined specimens. They are exclusively assigned to *Microtus*, which includes an extinct species (*M. epiratticepoides*) as well as a living species (*M.*

Table 7. Mammalian faunas of each site in Yage Quarry. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth is shown. Additionally, black circle (●) indicates the occurrence known from other parts. The fossiliferous sediments of Site 3 are considered to be Middle Pleistocene in age, while those of other sites are of Late Pleistocene age.

TAXON	SITE											
	Site 1	Site 2	Site 3	Site 4-a	Site 4-b	Site 4-c	Site 4-d	Site 4-e	Site 4 (exact fissure unknown)	Site 5	Site 6	Site unknown
INSECTIVORA												
<i>Crociodura dsinezumi</i>	1	-	-	-	-	-	-	-	-	-	-	-
** <i>Anourosorex japonicus</i>	1	-	-	-	-	-	-	-	1	-	-	-
<i>Urotrichus talpoides</i>	8	-	-	1	-	-	1	-	3	26	-	1
<i>Mogera</i> sp. A (small form)	-	-	-	●	-	-	●	2	-	9	-	●
<i>Mogera</i> sp. B (large form)	-	-	-	-	-	-	-	-	-	1	-	-
CHIROPTERA												
<i>Rhinolophus cornutus</i>	-	-	-	●	-	-	3	-	2	●	-	1
<i>Rhinolophus ferrumequinum</i>	15	-	12	●	-	●	-	3	38	18	4	7
<i>Myotis macrodactylus</i>	-	-	-	-	●	-	-	-	6	-	-	-
<i>Myotis</i> sp.	2	-	-	●	-	-	-	1	-	●	-	-
<i>Miniopterus schreibersii</i>	-	-	-	●	-	-	-	30	-	●	-	-
<i>Murina leucogaster</i>	-	-	-	●	-	-	-	-	-	●	-	1
PRIMATES												
<i>Macaca fuscata</i>	-	-	-	-	-	-	-	-	-	-	-	●
RODENTIA												
<i>Phaulomys</i> cf. <i>smithii</i>	-	-	-	-	-	-	-	1	-	-	-	-
<i>Microtus montebelli</i>	2	1	-	-	-	-	-	1	1	4	-	3
** <i>Microtus epiratticepoides</i>	1	-	-	-	-	-	-	-	-	-	-	-
** <i>Microtus</i> cf. <i>brandtioides</i>	-	-	-	-	-	-	-	-	-	1	-	-
<i>Microtus</i> sp. indet.	1	1	-	-	-	-	2	-	-	4	-	2
<i>Apodemus speciosus</i>	-	1	-	-	-	-	2	3	5	2	1	-
<i>Apodemus argenteus</i>	-	2	-	-	-	-	2	-	-	-	1	-
CARNIVORA												
<i>Nyctereutes procyonoides</i>	-	-	-	-	-	-	-	-	-	●	-	●
* <i>Ursus arctos</i>	-	-	-	-	-	-	-	-	-	●	-	-
<i>Meles meles</i>	1	-	-	-	-	-	-	-	-	-	-	●
ARTIODACTYLA												
<i>Cervus</i> sp.	-	-	-	●	-	2	4	3	1	3	-	1

* exotic form to Honshu; ** extinct form.

montebelli).

The insectivores are composed of four species. In the examined specimens, *Urotrichus talpoides* is most abundant, while an extinct species (*Anourosorex japonicus*) is rare. Moreover high-mountain forms are absent. The chiropterans are exclusively represented by *Rhinolophus ferrumequinum* and *Myotis* sp. The former is more abundant than the latter.

The composition of the present fauna indicates the temperate forests which were developed under similar climatic conditions to those in the present day.

Site 2 ———

The examined materials are restricted to only five mandibles of rodents which are assigned

to three living species (excluding *Microtus* sp. indet.; see Table 7). In addition to these, TOMIDA (1978) reported the following 12 forms from the "Upper Yage Formation" of Fissures A and B which possibly correspond to this site:

1. *Anourosorex japonicus* SHIKAMA et HASEGAWA
2. *Mogera* sp.
3. *Rhinolophus ferrumequinum* (SCHREBER)
4. *Macaca fuscata* (BLYTH)
5. *Canis lupus* LINNAEUS
6. *Nyctereutes procyonoides* (GRAY)
7. *Ursus arctos* LINNAEUS
8. *Mustela sibirica* PALLAS
9. *Meles meles* (LINNAEUS)
10. *Panthera tigris* (LINNAEUS)
11. *Cervus praenipponicus* SHIKAMA
12. *Sinomegaceros yabei* (SHIKAMA)

Of these, 1, 11 and 12 are extinct species, while 5 and 10 are exotic species to the Japanese Islands. As a whole, the present fauna indicates the similar climatic and vegetational conditions to those suggested by the fauna of Site 1.

Site 4 —

Table 7 shows the abundance of each mammalian form in accordance with the subdivision of this site (4-a to 4-e). However the specimens which bear no records of the subdivision are also found in the examined materials. They are shown as Site 4 (exact fissure unknown) in the table.

The sediments of Site 4-a yield eight forms of mammals which are poor in number and contain no rodents. Of these, five forms belong to Chiroptera. The mammalian remains of Sites 4-b and 4-c are very scarce. They are exclusively assigned to two living chiropteran species. The fossil assemblage of Site 4-d comprises seven forms of mammals which contain three rodent forms. The number of specimens is few in all the forms. In Site 4-e, eight forms of mammals are recognized. In comparison with Sites 4-a to 4-d, the specimens are considerably abundant. In the assemblage of this site, *Miniopterus schreibersii* is highly predominant. On the other hand, the rodent remains are much fewer than this species, but are assigned to three forms.

The specimens without any records of the subdivision are assigned to eight forms which include *Anourosorex japonicus*, the only extinct species in Site 4. In these specimens, *Rhinolophus ferrumequinum* is predominant. However the rodents which comprise only two species are much fewer than *R. ferrumequinum*.

Site 4 presumably corresponds to Fissure J of TOMIDA (1978). In addition to the mammals listed in Table 7, he recorded the occurrence of the following species from Fissure J:

- Mogera wogura* (TEMMINCK)
Mustela sibirica PALLAS

As a whole, the fauna of Site 4 is characterized by the abundant occurrence and greater variety of the chiropterans. Because the composition of the fauna is almost identical with that of the lowland fauna of the present Honshu, it possibly suggests the similar vegetational and climatic conditions to those in the present day.

Site 5 —

The examined materials are assigned to 14 forms of mammals, which contain three forms of rodents (excluding *Microtus* sp. indet.). *Microtus* is predominant in the rodent fauna, and includes an extinct form, *M. cf. brandtioides*. In the assemblage of insectivores, *Urotrichus talpoides* is most abundant, while the remaining two forms (*Mogera* sp. A and B) are fewer*. The co-existence of the two forms of *Mogera* should be noticed. The high-mountain forms are absent from the insectivore assemblage. The chiropterans comprise five forms, in which *Rhinolophus ferrumequinum* is most abundant.

The carnivore and artiodactyl remains are assigned to three forms. In addition to these, TOMIDA (1978) reported the following forms from his "Upper Yage Formation" of Fissures D and K which possibly correspond to Site 5:

Mustela sibirica PALLAS

Panthera tigris (LINNAEUS)

Equus sp.

Cervus praenipponicus SHIKAMA

Of these seven forms, *Ursus arctos* and *P. tigris* are exotic forms to Honshu and to the Japanese Islands respectively, while *C. praenipponicus* is extinct.

The ratio of extinct forms plus exotic forms to Japan is estimated as 19% in all taxa and 15% in other orders than rodents**. The climatic and vegetational conditions inferred from the faunal composition are similar to those in the present Honshu.

Site 6 —

The sediments of this site yield only six identifiable specimens. They are assigned to three living species of micro-mammals (Table 7).

7. East Fissure of Suse Quarry

Fifteen forms of mammals are obtained from this fissure (excluding *Microtus* sp. indet. and *Cervus* sp. indet.). They include one extinct species only. The abundance of each form is shown in Table 6. Because the micro-mammals are highly predominant in the assemblage of this fissure, the relative abundance of each micro-mammalian taxon estimated from the number of mandibles is shown in Fig. 66.

Rodent fauna —

The rodent remains are assignable to five forms which are now found in the lowlands of central Honshu. Of these, *Apodemus speciosus* is most abundant, while others are much fewer.

Associated fauna —

The insectivore fauna comprises four lowland forms. Of these, *Urotrichus talpoides* is most abundant. The chiropterans and primates are referred to a single species each. The materials of these species are scarce. The carnivore remains are poor in variety and number. They are assigned to only two species. The artiodactyls are represented by *Cervus* only, but its remains are relatively abundant. MATSUHASHI (1977) identified an antler and a mandible as

* Recently the remains of *Arvicolax japonicus* are found in the additional materials of this site.

** *Microtus* sp. indet., *Equus* sp. and *Cervus* sp. are excluded from the calculation.

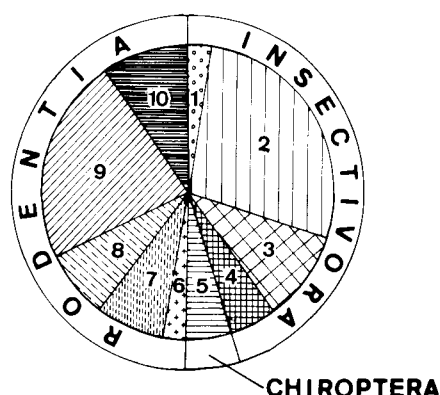


Fig. 66. Composition of the micro-mammalian fossils obtained from East Fissure of Suse Quarry. The ratio of the number of mandibles is shown (total=40).

1, *Crociodura dsinezumi*; 2, *Urotrichus talpoides*; 3, *Mogera* sp. B (large form); 4, *M.* sp. A (small form); 5, *Rhinolophus ferrumequinum*; 6, *Petaurista leucogenys*; 7, *Phaulomys* cf. *smithii*; 8, *Microtus montebelli*; 9, *Apodemus speciosus*; 10, *A. argenteus*.

an extinct species, *C. praenipponicus*.

General remarks —

The faunal composition is well coincident with that of the lowland fauna of the present central Honshu. Therefore it is assumed that the climatic and vegetational conditions were similar to those in the present day, when the sediments of this fissure were deposited.

8. Kannondo Cave Site (Late Pleistocene horizons)

Forty forms of mammals are recognized in the fossil assemblage of these horizons. They contain five to seven extinct forms and one exotic form to the Japanese Islands. The abundance of the mammalian remains in each horizon is shown in Figs. 67 and 68 as well as in Table 8.

Rodent fauna —

The rodent remains are assignable to ten forms. *Phaulomys* cf. *smithii* and *Microtus montebelli* are abundant in comparison with other forms. The former form remarkably increases from Horizon P to the lower part of M, and then somewhat decreases toward the upper part of M. On the contrary, the latter shows a tendency that the frequency decreases from Horizons P to M. *Apodemus speciosus* and *A. argenteus* are other dominant elements, but generally less abundant than those arvicolids. *A. speciosus* occurs in relatively low frequency from Horizons P to N, but remarkably increases from Horizon N to the upper part of M. On the other hand, *A. argenteus* considerably increases from Horizon P to the lower part of O, and then gradually decreases toward Horizon M.

Two extinct arvicolids (*M. epiratticepoides* and *M.* cf. *brandtioides*) are much fewer than the extant species, *M. montebelli*. *M. epiratticepoides* is remarkably diminished from the upper part of

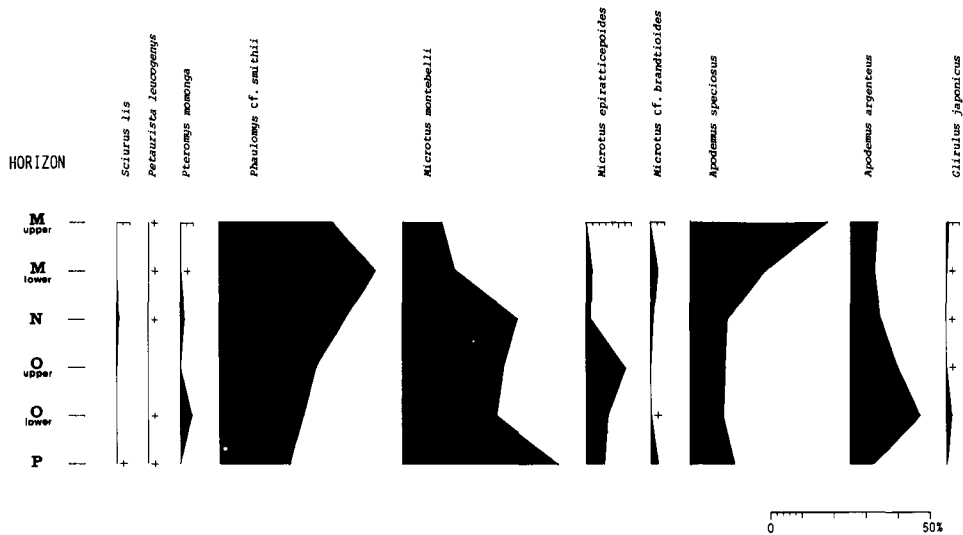


Fig. 67. Diagram showing the relative abundance of each form of rodents in the Late Pleistocene horizons of Kannondo Cave Site. The specimens collected by the screening method in the 16th to 19th excavations were examined. The abundance is calculated by the number of M_1 in each horizon. Cross (+) indicates the occurrence known from other teeth and bones.

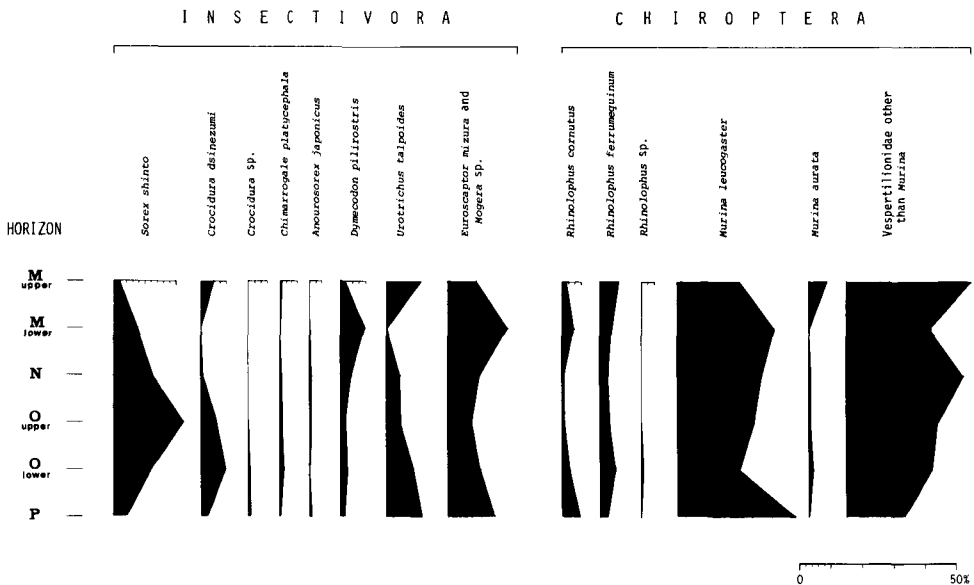


Fig. 68. Diagram showing the relative abundance of each form of insectivores and chiropterans in the Late Pleistocene horizons of Kannondo Cave Site. The specimens collected by the screening method in the 16th to 19th excavations were examined. The abundance is calculated by the total number of skull (mostly fragmental maxilla), mandible and isolated tooth in each horizon.

Table 8. Stratigraphic distribution of lagomorphs and middle- and large-sized mammals in the Late Pleistocene horizons of Kannondo Cave Site. The specimens obtained by the 12th to 14th excavations were examined. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth is shown in each taxon and in each horizon. The occurrence known from other bones is designated by black circle (●).

HORIZON \ TAXON	PRIMATES	LAGOMORPHA	CARNIVORA	PROBOSCIDEA	ARTIODACTYLA	OTHER
	<i>Macaca fuscata</i>	<i>Lepus brachyurus</i>	<i>Canis</i> sp. <i>Vulpes vulpes</i> <i>Nyctereutes procyonoides</i> * <i>Ursus</i> sp. <i>Mustela sibirica</i> <i>Mustela</i> sp. <i>Martes</i> sp. <i>Meles meles</i> © <i>Panthera</i> cf. <i>pardus</i>	** <i>Elephantidae</i> gen. et sp. indet.	<i>Sus scrofa</i> ** <i>Cervus praenipponicus</i> <i>Cervus</i> sp. indet.	
horizon unknown	●	-	● - 1 - - - ● 1 -	-	3 - 7	
M (upper)	1	-	- - - - - - 1 -	-	- - ●	
N	-	-	- - - 1 - - - - -	1	1 - ●	
O (upper)	6	27	● ● 5 2 - ● ● 1 2	8	1 1 450	
O (lower)	-	4	- - 1 1 ● - ● - 1	-	- - 84	
P	-	-	- - ● 1 - - - - -	-	- - 8	

* exotic form to Honshu; ○ exotic form to Japan; ** extinct form.

Horizon O to N, and moreover it is completely absent from the upper part of M. On the other hand, *M. cf. brandtioides* occurs in Horizon P, the lower part of O, N and the lower part of M in extremely low frequency. This form does not appear in the upper part of M. Because these two extinct forms are also absent from the Holocene horizons of this site, they were possibly extinguished from this area at the time between the lower part of Horizon M and its upper part.

The sciurids and glirids are represented by three and one species respectively. They occur in most horizons, but are poor in number.

Associated fauna —

The insectivore remains are assigned to nine forms. Among these, *Sorex shinto* and *Mogera* sp. are abundantly found. *Sorex shinto* increases from Horizon P to the upper part of O, and then decreases toward the upper part of M. *Crociodura dsinezumi* is less abundant than *S. shinto*. It becomes rare in Horizon N and the lower part of M. *Crociodura* sp. is distinguishable from *C.*

dsinezumi by its smaller size. It occurs in Horizon P and the lower part of O in extremely low frequency. This form may be exotic to the Japanese Islands.

Chimarrogale platycephala is absent from the lower part of Horizon M, but occurs in other horizons. *Anourosorex japonicus* is the only extinct species in the insectivore fauna. It is rarely found in Horizon P, the upper part of O and N, but absent from M and the Holocene horizons. Therefore it is inferred that this species was extinguished at the time between Horizon N and the lower part of M.

Dymecodon pilirostris uncommonly occurs in Horizons P and O, and gradually increases toward the lower part of M. It again decreases from this horizon to the upper part of M. On the contrary, *Urotrichus talpoides* decreases from Horizon P to the lower part of M, but then remarkably increases toward the upper part of M. *Euroscaptor mizura* is much fewer than *Mogera* sp. which shows affinity with *M. wogura*.

The chiropterans are composed of at least seven forms. The vespertilionids are much more abundant than the rhinolophids. In the former family, *Murina leucogaster* and *Myotis* sp. are highly predominant, while *Murina aurata* and *Miniopterus schreibersii* are scarce. In the latter family, *Rhinolophus ferrumequinum* is generally more abundant than *R. cornutus*. *Rhinolophus* sp. is found in the lower part of Horizon O in very low frequency. It approximates *R. ferrumequinum* in size, but morphologically different from this species.

The primate remains are exclusively assigned to *Macaca fuscata*. They are obtained from the upper parts of Horizons M and O. The lagomorphs are restricted to a single species, *Lepus brachyurus*, which is commonly found in Horizon O.

The carnivores are rich in variety (seven forms), but poor in abundance. The specimens assigned to *Ursus* sp. are comparable with *Ursus arctos* which is absent from the fauna of the present Honshu. This form rarely occurs in Horizons P to N. *Panthera* cf. *pardus* is evidently exotic to the Japanese Islands. It is uncommonly found in Horizon O.

The proboscideans are exclusively represented by small cheek tooth fragments obtained from Horizon N and the upper part of O. These fragments show the characters of Elephantiidae in the micro-structure of enamel (KAMIYA and KAWAMURA, 1981).

The artiodactyl remains are exclusively assigned to *Sus scrofa* and *Cervus*. The former occurs in Horizon N and the upper part of O, but is extremely rare. On the other hand, *Cervus* are abundantly found in all the horizons. The specific determination of the remains of *Cervus* is difficult, because well-preserved antlers are very scarce. Only one fragmental antler from the upper part of Horizon O is presumably assignable to *C. praenipponicus*.

General remarks —

The ratio of extinct forms plus exotic forms to Japan ranges from 15% to 20% in all taxa, and from 13% to 20% in other orders than rodents. These values approximate the ratios in F₄ of Kumaishi-do Cave and in Site 5 of Yage Quarry, but are obviously higher than those in the Holocene localities of Japan.

Because various forest dwellers occur in all the horizons, it is assumed that sylvan environments predominated when the sediments of these horizons were deposited. On the other hand, the predominance of *Microtus* in Horizon P suggests that the forests were relatively

open and grasslands were partly developed. The decrease of *Microtus* toward the upper horizons also indicates the development of dense forests in relation to the reduction of the grasslands.

Because the high-mountain forms abundantly occur in Horizon P to the lower part of M, it is inferred that the climate was colder in the periods of these horizons than in the present day. On the other hand, these forms remarkably decrease in the upper part of Horizon M. This fact suggests that the climate presumably became warmer when the sediments of this horizon were deposited.

9. Locality 2 of Ube Kosan Quarry

As shown in Table 6, eight forms of micro-mammals are obtained from this locality (excluding *Microtus* sp. indet.). In these, only one extinct species is included (*Microtus epiratticepoides*).

Rodent fauna —

The rodent remains are assigned to four forms. Of these, *Apodemus argenteus* is most abundant, which slightly exceeds *A. speciosus* in number. These murids are much more abundant than the arvicolids which comprise one M_1 of *Clethrionomys-Phaulomys* group and three molars of *Microtus*. The former specimen is unrooted, and therefore it is indeterminable whether the specimen is assigned to *Phaulomys* or a younger individual of *Clethrionomys*.

Associated fauna —

Insectivora is represented by a single fragmental mandible which is assignable to *Urotrichus talpoides*. The chiropteran remains are also poor in number, but referred to three species.

General remarks —

Although the fauna of this locality is insufficient in variety and abundance for detailed discussion, the faunal composition roughly indicates the sylvan environments which are similar to those in the present day.

10. Seiryukutsu Cave

The mammalian assemblage is composed of 13 forms (excluding *Microtus* sp. indet.; Tables 9, 10). In these, two extinct forms are included.

Rodent fauna —

Three forms of rodents are recognized, which contain neither extinct nor exotic species. Among these, *Phaulomys* cf. *smithii* is predominant.

Associated fauna —

The insectivores comprise five forms. Of these, *Sorex* cf. *shintō* is most abundant, while *Urotrichus talpoides* is next in abundance. However other forms are very scarce. The chiropterans are abundant in comparison with the insectivores, and comprise three species. Among these three, *Rhinolophus ferrumequinum* is highly predominant. As regards large-sized mammals, *Palaeoloxodon naumanni* and *Cervus nippon* are known from this assemblage.

General remarks —

The abundant occurrence of sylvan inhabitants (*Urotrichus talpoides*, *Phaulomys* cf. *smithii*,

Table 9. Faunas of micro-mammals from the caves of the Hirao-dai Plateau. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth assignable to each taxon is shown. The occurrence recorded by other bones is marked by black circle (●). +, presence shown by HASEGAWA *et al.* (1968), SOTSUKA (1972a, b) and KAWAMURA and SOTSUKA (1984).

TAXON \ LOCALITY										
	Seiryukutsu Cave	Hirao-ana Cave	Ohera-ana Cave	Ninjinkubo First Cave	Yakubono-ana Cave	Mejiro-do Cave	Ojika-do Cave			Yoshigatani Third Cave
							Chamber 1	Chamber 2	Branch 1	
INSECTIVORA										
* <i>Sorex cf. shinto</i>	6	—	—	—	—	—	—	—	—	—
** <i>Anourosorex cf. japonicus</i>	1	—	—	—	—	—	—	—	—	—
<i>Crociodura dsinezumi</i>	1	—	1	1	—	—	—	—	—	—
<i>Urotrichus talpoides</i>	4	—	—	2	—	—	+	—	2	—
<i>Euroscaptor mizura</i>	—	—	—	●?	—	—	—	—	—	—
<i>Mogera wogura</i>	—	—	—	—	—	—	+	—	—	—
<i>Mogera</i> sp.	2	—	4	2	—	—	—	—	2	—
CHIROPTERA										
<i>Rhinolophus cornutus</i>	11	—	—	1	—	—	—	—	—	—
<i>Rhinolophus ferrumequinum</i>	39	—	3	224	—	—	+	—	9	4
<i>Myotis macrodactylus</i>	—	—	—	9	—	—	—	3	●	—
<i>Miniopterus schreibersii</i>	4	—	—	1?	—	—	—	—	—	—
<i>Murina leucogaster</i>	—	—	—	53	—	—	—	3	5	—
LAGOMORPHA										
<i>Lepus brachyurus</i>	—	1	—	13	+	—	+	—	—	+
RODENTIA										
<i>Petaurista leucogenys</i>	—	—	—	7	—	+	2	—	1	+
<i>Phaulomys cf. smithii</i>	16	—	—	31	1	7	1	1	4	21
<i>Microtus montebelli</i>	1	—	3	—	—	—	—	—	—	1
<i>Microtus</i> sp. indet.	7	—	3	—	—	—	—	—	1	—
<i>Apodemus speciosus</i>	—	—	1	9	—	—	—	—	—	3
<i>Apodemus argenteus</i>	2	—	—	47	1	—	—	—	7	—

* exotic form to this area. ** extinct form.

Apodemus argenteus etc.) in this assemblage suggests the woodland environments which are similar to those in the present west Japan. Moreover it is inferred that the climate is cooler than in the present day, because a high mountain form (*Sorex cf. shinto*) which is now absent from Kyushu occurs in high frequency.

11. Mejiro-do Cave

The mammalian remains are poor in number, but assignable to six forms (Tables 9, 10). Of these, *Phaulomys* cf. *smithii* is identified by the author, while the occurrence of other forms is cited from SOTSUKA (1972b). These six forms comprise five living species which are now distributed in Kyushu and one extinct form (*Sinomegaceros* sp.).

Table 10. Faunas of large mammals from the caves of the Hirao-dai Plateau. The data are cited from HASEGAWA *et al.* (1968, 1980), SOTSUKA (1972a, b), and KAWAMURA and SOTSUKA (1984).

TAXON	LOCALITY									
	Seiryukutsu Cave	Hirao-ana Cave	Ohera-ana Cave	Ninjinkubo First Cave	Yakubono-ana Cave	Mejiro-do Cave	Chamber 1	Ojika-do Cave Chamber 2	Branch 1	Oiwa-ana Cave Yoshigatani Third Cave
PRIMATES										
<i>Macaca fuscata</i>	-	-	-	+	-	-	+	+	+	-
<i>Homo sapiens</i>	-	-	-	+	-	-	-	+	-	-
CARNIVORA										
◦ <i>Canis lupus</i>	-	+	-	-	-	-	-	-	-	-
<i>Canis familiaris</i>	-	-	+	+	-	-	+	-	-	-
<i>Nyctereutes procyonoides</i>	-	-	+	-	-	+	-	-	+	+
<i>Meles meles</i>	-	+	+	+	+	-	+	+	+	+
◦ <i>Lutra lutra</i>	-	-	-	-	-	-	+	-	-	-
PROBOSCIDEA										
** <i>Palaeoloxodon naumanni</i>	+	-	-	-	-	-	-	-	-	-
ARTIODACTYLA										
<i>Sus scrofa</i>	-	-	-	+	+	+	+	+	+	-
** <i>Sus nipponicus</i>	-	-	-	-	-	-	-	-	-	+
<i>Cervus nippon</i>	+	+	-	+	+	+	+	-	+	-
** <i>Sinomegaceros</i> sp.	-	-	-	-	-	+	-	-	-	-
<i>Capra hircus</i>	-	-	-	-	-	-	-	-	-	+

○ form which was extinguished from this area very recently. ** extinct form.

12. Minatogawa Site

The materials examined in the present study are assigned to the following forms:

Tokudaia osimensis (ABE)

Diplothrix legata (THOMAS)

Sus sp.

Cervus astylodon (MATSUMOTO)

In addition to these, HASEGAWA (1980a) listed the following mammals:

? *Rhinolophus cornutus* (TEMMINCK)

Muntiacinae, gen et sp. indet.

The rodents are restricted to two endemic species to the Ryukyu Islands (*T. osimensis* and *D. legata*). The former species is abundantly found in the materials, while the latter is scarce. Such a tendency is coincident with the description by HASEGAWA (1980a, Table 2). He also gave the relative abundance of other forms. According to him, *Sus* sp. (= ? *Sus leucomystax taiwanus* in his paper) commonly occurs, while ? *R. cornutus*, *C. astylodon* and Muntiacinae gen. et sp. indet. are rare.

13. Kuteken

The following mammals are obtained from this quarry:

Tokudaia osimensis (ABE)

Sus sp.

Cervus astylodon (MATSUMOTO)

? Muntiacinae gen. et sp. indet.

All of these forms are also found in Minatogawa Site. The rodent remains are not abundant, and exclusively assigned to *T. osimensis*. Other mammals are less abundant than *T. osimensis*.

14. Iso

The examined materials are few and assigned to *Tokudaia osimensis* only. Additionally OSHIRO and NOHARA (1977) reported the occurrence of suid and cervid remains.

15. Gajanbira

The examined materials are exclusively assigned to the following rodents:

Tokudaia osimensis (ABE)

Diplothrix legata (THOMAS)

The former is more abundant than the latter. Additionally the occurrence of suids and cervids was reported from this locality by OSHIRO and NOHARA (1977).

C. Holocene localities

1. West Fissure of Suse Quarry

The mammalian remains obtained from this fissure are assigned to 12 forms which include neither extinct nor exotic forms (Table 6).

Rodent fauna —

The rodent fauna is poor in variety in comparison with that of East Fissure of this quarry. Namely the rodent remains are restricted to *Apodemus speciosus* and *A. argenteus* which are dominant murids in the present Honshu. The former species are much more abundant than the latter.

Associated fauna —

The insectivores are composed of three forms. Of these, *Urotrichus talpoides* is most abundant, while two forms of *Mogera* (smaller and larger forms) are scarce. The lagomorph remains are assigned to a single species (*Lepus brachyurus*). They are rather abundantly found. In comparison with other orders, the carnivores are rich in variety (four species). Among these, *Nyctereutes procyonoides* and *Meles meles* are relatively abundant, while the remaining two species are rare. The artiodactyls are represented by *Sus scrofa* and *Cervus* sp. The former is more abundant than the latter.

General remarks —

As a whole, the assemblage shows great similarity to the fauna of the present central Honshu. Therefore it is inferred that the environments were similar to those in the present day, when the sediments of this fissure were deposited. In contrast with the fauna of East

Fissure of the same quarry, *Sus* is abundantly found in the present assemblage. This possibly indicates that the sediments of this fissure are younger than those of East Fissure. Such a presumption is well coincident with the results of the fluorine test.

2. Kitoragawa Site

The following mammals were found in the fossiliferous sediments of this site:

Microtus montebelli (MILNE-EDWARDS)

Apodemus speciosus (TEMMINCK)

Rattus sp.

Canis familiaris LINNAEUS

Lutra lutra (LINNAEUS)

Sus scrofa LINNAEUS

Cervus nippon TEMMINCK

The rodent remains are poor in number (1 mandible, 13 molars and 10 incisors), but are assigned to three forms. Of these, *Microtus montebelli* is most abundant, and *Apodemus speciosus* is next in abundance. However *Rattus* sp. is restricted to only one specimen.

The carnivores (*Canis familiaris* and *Lutra lutra*) are rarely found, while the artiodactyls (*Sus scrofa* and *Cervus nippon*) are abundant. This suggests that these artiodactyls were hunted as the main games of ancient men.

3. Domen Cave Site

As shown in Tables 11 and 12, the examined materials are assigned to 23 forms of

Table 11. Abundance of each mammalian form in the materials collected by the tentative, first to seventh, ninth and tenth excavations of Domen Cave Site. The number of the specimens assigned to each taxon is shown.

TAXON HORIZON																																																			
		INSECTIVORA		<i>Urotrichus talpoides</i>		<i>Mogera</i> sp.		CHIROPTERA		<i>Rhinolophus ferrumequinum</i>		PRIMATES		<i>Macaca fuscata</i>		LAGOMORPHA		<i>Lepus brachyurus</i>		RODENTIA		<i>Petaurista leucogenys</i>		<i>Apodemus speciosus</i>		<i>Apodemus argenteus</i>		CARNIVORA		<i>Canis lupus</i>		<i>Canis familiaris</i>		<i>Vulpes vulpes</i>		<i>Nyctereutes procyonoides</i>		<i>Mustela sibirica</i>		<i>Martes melampus</i>		<i>Meles meles</i>		<i>Lutra lutra</i>		ARTIODACTYLA		<i>Sus scrofa</i>		<i>Cervus</i> sp.	
horizon unknown		—	1		3		—		29		2	—	—		—	5	1	19	—	—	1	1		71	254																										
I		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	12																										
III		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	2	12																										
IV		—	—	—	1	—	—	—	4	—	—	—	—	—	—	—	—	6	—	—	—	—	—	36	29																										
V		1	2	15	3	28	5	3	1	2	5	6	82	1	1	3	—	199	520																																

mammals (excluding *Microtus* sp. indet.). They include only one exotic species (*Canis lupus*). These materials are mostly obtained from Horizon V.

Rodent fauna —

The rodent fauna of Horizon V comprises five forms. Of these, *Phaulomys* cf. *smithii* is most abundant. This form is followed by *Apodemus speciosus* which is slightly more abundant than *Microtus* (*M. montebelli* plus *M.* sp. indet. in Table 12). However *A. argenteus* and *Petaurista leucogenys* are much fewer than *Microtus*.

The rodent remains are not obtained from other horizons, although the remains of unknown horizon are also present.

Associated fauna —

The insectivore remains from Horizon V are assigned to five forms which include no high-mountain forms. Of these, *Urotrichus talpoides* is most abundant, while *Mogera* sp. B is next in abundance. The remaining three forms are much fewer than these two forms. *U. talpoides* and *M.* sp. B also occur as the specimens of unknown horizon.

The chiropterans comprise *Rhinolophus ferrumequinum* and *Murina leucogaster* in Horizon V.

Table 12. Total number of skull (mostly fragmental maxilla), mandible and isolated tooth of micro-mammals collected from Domen Cave Site by the washing and screening method in the 13th and 15th excavations.

HORIZON & LAYER		TAXON														
		INSECTIVORA					CHIROPTERA		LAGOMORPHA		RODENTIA					
		<i>Crociodura dsinezumi</i>	<i>Chimarrogale platycephala</i>	<i>Urotrichus talpoides</i>	<i>Mogera</i> sp. A (small form)	<i>Mogera</i> sp. B (large form)	<i>Rhinolophus ferrumequinum</i>	<i>Murina leucogaster</i>	<i>Lepus brachyurus</i>	<i>Petaurista leucogenys</i>	<i>Phaulomys</i> cf. <i>smithii</i>	<i>Microtus montebelli</i>	<i>Microtus</i> sp. indet.	<i>Apodemus speciosus</i>	<i>Apodemus argenteus</i>	
Horizon unknown		-	-	6	-	3	1	2	5	1	2	-	4	4	-	
Horizon V	10-upper	2	-	3	-	4	7	-	-	-	22	-	16	14	3	
	10-shell-bed	2	-	3	1	-	-	-	1	-	19	-	2	9	3	
	10-lower	-	-	4	1	8	-	1	-	-	6	-	3	1	2	
	11	-	-	5	-	1	1	-	-	-	18	-	4	2	-	
	12-upper	-	1	1	2	-	6	-	-	-	18	1	1	3	-	

The former species is much more abundant than the latter. *R. ferrumequinum* also occurs in Horizon IV and as the specimens of unknown horizon.

The primates and lagomorphs are assigned to a single species each. *Macaca fuscata* is scarcely found in Horizon V, while *Lepus brachyurus* is much more abundant and occurs in Horizons IV and V. Many specimens of unknown horizon are also assigned to the latter species.

The carnivore remains from Horizon V are assigned to eight species. Of these, *Nyctereutes procyonoides* is highly predominant. It is also obtained from Horizons III and IV. On the other hand, *Canis lupus* is rarely found in Horizon V. This species was extinguished from the Japanese Islands at the beginning of this century, but is now present in the continent. Therefore it is formally regarded as an exotic species to the islands. The carnivore remains of unknown horizon are assigned to five species as shown in Table 11.

In comparison with other orders, the artiodactyls are very abundant in Horizons I, III, IV and V as well as in the specimens of unknown horizon. They are exclusively assigned to *Sus scrofa* and *Cervus* sp. The former species is generally less abundant than the latter.

General remarks —

The ratio of extinct forms plus exotic forms to Japan is estimated as 0% in all taxa as well as in other orders than rodents, when *Canis lupus* is excluded. Because the faunal composition of the assemblage of Horizon V is almost identical with that of the lowland fauna of the present Honshu, this assemblage indicates that the vegetational and climatic conditions at the time of Horizon V are nearly equal to those in the present day.

4. Anagami Rockshelter Site

The examined mammalian remains are assigned to 16 forms (excluding *Microtus* sp. indet.) which contain neither extinct nor exotic forms (Table 13). Because the specimens are relatively few in each layer, the fauna of this site is described altogether.

Rodent fauna —

The rodents are composed of five forms. Of these, *Petaurista leucogenys* is most abundant. This seems to be resulted from the hunting of this animal by ancient men. *Apodemus speciosus* is next in abundance, which is followed by *Microtus*. Moreover the remaining two forms such as *Sciurus lis* and *Phaulomys* cf. *smithii* are rarely found.

Associated fauna —

The insectivores are composed of three forms which include no high-mountain forms. Of these, *Mogera* sp. is most abundant, while others are rare. The primates and lagomorphs are represented by *Macaca fuscata* and *Lepus brachyurus* respectively. The former is less abundant than the latter. The carnivore remains are assigned to four forms, of which *Nyctereutes procyonoides* is most abundant. The artiodactyl remains are rich in number, and are assigned to *Sus scrofa* and *Cervus* sp. The frequency of the former approximates to that of the latter.

General remarks —

The fauna of this site is nearly equal to the lowland fauna of the present Honshu. Therefore it can be stated that the climatic and vegetational conditions inferred from the

Table 13. Faunal composition of the mammalian remains from Anagami Rockshelter Site. These remains were collected in the first excavation, and by the screening procedure in the third excavation. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth is shown. Additionally, black circle (●) indicates the occurrence known from other parts.

GRID & LAYER	TAXON																
		INSECTIVORA	<i>Crociodura dsinezumi</i>	<i>Urotrichus talpoides</i>	<i>Mogera</i> sp.	PRIMATES	<i>Macaca fuscata</i>	LAGOMORPHA	<i>Lepus brachyurus</i>	RODENTIA	<i>Sciurus lis</i>	<i>Petaurista leucogenys</i>	<i>Phaulomys</i> cf. <i>smithii</i>	<i>Microtus montebelli</i>	<i>Microtus</i> sp. indet.	<i>Apodemus speciosus</i>	CARNIVORA
																	<i>Vulpes vulpes</i>
																	<i>Nyctereutes procyonoides</i>
																	<i>Mustela sibirica</i>
																	<i>Meles meles</i>
																	ARTIODACTYLA
																	<i>Sus scrofa</i>
																	<i>Cervus</i> sp.
A-0, A-1, B-0, B-1	horizon unknown	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-
	1	-	-	1	1	-	-	-	-	3	-	-	-	-	-	-	●
	2	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	●	●	-	-	2	●	2	-	-	-	-	-	-	-	-
	4	-	-	1	2	3	-	2	-	2	-	3	-	2	1	●	9
	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●
	6	-	-	●	-	-	-	-	-	1	-	-	-	-	1	-	●
B-2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	●
	2	-	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-
	3	-	-	-	-	-	-	-	-	1	-	1	1	-	-	-	-

composition of the fauna are almost identical with those in the present day.

5. Kannondo Cave Site

As shown in Tables 14 and 15, 32 forms of mammals are obtained from the Holocene horizons of this site (excluding *Microtus* sp. indet. and *Rattus* sp. indet.). They contain two exotic forms to Japan.

Rodent fauna —

The rodent remains are assigned to seven forms. They are rich in number and variety in the lower horizons (H to L), but are relatively poor and biased in the upper horizons (A to G). *Petaurista leucogenys* is the largest rodent in the present assemblage, and seems to have been hunted by ancient men. Therefore the pattern of its stratigraphic distribution is concordant with those of the middle- and large-sized mammals such as *Nyctereutes procyonoides*, *Sus scrofa* and *Cervus nippon*. Namely *P. leucogenys* increases in Horizons C, F, G and H as in these middle-

and large-sized mammals. Other rodents are much smaller than *P. leucogenys*, and are concentrated in Horizons I to L. Of these, *Apodemus speciosus* is most abundant, while *Microtus* is next in abundance. *Phaulomys* cf. *smithii* and *A. argenteus* are less abundant than *Microtus*, but considerably exceed *Glirulus japonicus* in number. The remains of *Rattus* are rarely obtained from Horizons C and D. If they are assigned to *R. rattus* or *R. norvegicus*, this animal was possibly commensal with the ancient men in the periods of these horizons.

Associated fauna —

The insectivore remains are relatively scarce, and are restricted to Horizons I to L excepting the specimens of unknown horizon. They are assigned to three forms which include no high-mountain forms.

The chiropterans are also poor in number, but relatively rich in variety (six forms). All the forms except *Rhinolophus ferrumequinum* are restricted to Horizons I to L, but *R. ferrumequinum*

Table 14. Stratigraphic distribution of micro-mammals in the Holocene horizons of Kannondo Cave Site. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth is shown. Additionally, black circle (●) indicates the occurrence known from other bones.

TAXON HORIZON	INSECTIVORA			CHIROPTERA		LAGOMORPHA		RODENTIA											
	<i>Crociodura dsinezumi</i>	<i>Urotrichus talpoides</i>	<i>Mogera</i> cf. <i>wogura</i>	<i>Rhinolophus cornutus</i>	<i>Rhinolophus ferrumequinum</i>	<i>Myotis</i> sp.	<i>Miniopterus schreibersii</i>	<i>Murina leucogaster</i>	<i>Murina aurata</i>	<i>Lepus brachyurus</i>	<i>Petaurista leucogenys</i>	<i>Phaulomys</i> cf. <i>smithii</i>	<i>Microtus montebelli</i>	<i>Microtus</i> sp. indet.	<i>Apodemus speciosus</i>	<i>Apodemus argenteus</i>	<i>Rattus norvegicus</i>	<i>Rattus</i> sp. indet.	<i>Glirulus japonicus</i>
horizon unknown	—	1	2	—	1	—	—	●	—	10	23	14	8	6	21	8	2	●	1
A	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
B	—	—	—	—	●	—	—	—	—	2	2	—	—	—	—	—	—	—	—
C	—	—	—	—	●	—	—	—	—	10	27	—	—	7	—	1	—	2	—
D	—	—	—	—	1	—	—	—	—	1	2	—	—	—	—	—	—	●	—
E	—	—	—	—	●	—	—	—	—	6	2	—	—	—	—	—	—	—	—
F	—	—	—	—	●	—	—	—	—	2	6	—	—	—	1	1	—	—	—
G	—	—	—	—	●	—	—	—	—	2	11	—	—	1	—	—	—	—	—
H	—	—	—	—	—	—	—	—	—	6	7	4	—	1	3	1	—	—	—
I	1	3	—	●	●	●	●	1	●	17	5	15	18	21	61	14	—	—	4
J	—	●	●	—	●	—	—	●	—	●	●	5	7	6	39	9	—	—	3
K	—	—	●	—	—	—	—	●	—	●	1	6	—	2	28	3	—	—	—
L	—	—	●	—	●	—	●	1	—	—	1	3	—	—	20	1	—	—	—

occurs in Horizons B to G, I, J and L.

The primates and lagomorphs are exclusively represented by *Macaca fuscata* and *Lepus brachyurus* respectively. The former is obtained from most horizons (C to K), but relatively poor in abundance. On the other hand, the latter is obtained from Horizons B to K. It is relatively abundant in Horizons C, E, H and I.

The carnivores are composed of 12 forms. Of these, *Nyctereutes procyonoides* is most abundant, while *Meles meles* is next in abundance. *Canis lupus* is an exotic species to Japan, and rarely occurs in Horizons C, E, H and I. *Lynx lynx* is another exotic species. It is also rarely found in Horizons G and I. The occurrences of *Mustela erminea* and *Lutra lutra* are rare. The former is obtained from Horizons C and I, while the latter comes from Horizons F and G. These two species are now extinct in west Honshu, but still living in other part of Japan.

The artiodactyls are abundant in comparison with the carnivores, but comprise three

Table 15. Stratigraphic distribution of middle- and large-sized mammals in the Holocene horizons of Kannondo Cave Site. Estimated minimum number of individuals (=maximum number of each bone or tooth in each horizon) is shown. The data are cited from ISHIDA (1978).

HORIZON \ TAXON																				TOTAL
		PRIMATES	<i>Macaca fuscata</i>	CARNIVORA																
				① <i>Canis lupus</i>	<i>Canis familiaris</i>	<i>Vulpes vulpes</i>	<i>Nyctereutes procyonoides</i>	<i>Selenarctos thibetanus</i>	<i>Mustela sibirica</i>	* <i>Mustela erminea</i>	<i>Martes melampus</i>	<i>Meles meles</i>	* <i>Lutra lutra</i>	① <i>Lynx lynx</i>	ARTIODACTYLA	<i>Sus scrofa</i>	<i>Cervus nippon</i>	<i>Capricornis crispus</i>		
A		-	-	1	-	1	-	-	-	-	1	-	-	-	1	2	-		6	
B		-	-	1	1	1	-	-	-	1	1	-	-	-	2	4	-		11	
C		1	1	1	1	19	1	-	1	1	5	-	-	-	13	31	2		77	
D		1	-	-	1	2	-	1	-	-	2	-	-	-	6	5	1		19	
E		3	1	-	1	3	-	-	-	1	2	-	-	-	8	9	1		29	
F		2	-	-	1	5	-	-	-	1	1	1	-	-	8	5	1		25	
G		2	-	1	1	10	-	-	-	2	4	2	1	-	25	21	2		71	
H		1	1	2	1	8	-	-	-	1	2	-	-	-	14	11	1		42	
I		2	1	1	-	12	1	-	1	4	3	-	1	-	13	11	1		51	
J		1	-	-	-	5	1	-	-	1	4	-	-	-	5	4	1		22	
K		1	-	-	-	1	1	-	-	-	1	-	-	-	2	3	1		10	
L		-	-	-	-	1	-	-	-	-	1	-	-	-	1	2	-		5	

* exotic form to west Honshu; ◉ exotic form to Japan.

species only. Among these, *Sus scrofa* and *Cervus nippon* are especially abundant, and occur in all the horizons. The ratio of the former species against the latter is variable in each horizon. Namely the former is more abundant mainly in the lower horizons (D and F to J), while it is less abundant mainly in the upper horizons (A to C, E, K and L). *Capricornis crispus* is obtained from Horizons C to K, but much fewer than other artiodactyl species.

General remarks —

The ratio of extinct forms plus exotic forms to Japan is estimated in Horizon I, because the remains from this horizon are richest in variety. The results are 4% in all taxa and 5% in other orders than rodents, when *Canis lupus* is excluded as in the case of Domen Cave Site.

This fauna is characterized by the absence of the extinct and high-mountain forms which are found in the Late Pleistocene horizons of the same site. Moreover its composition is well coincident with that of the lowland fauna of the present Honshu. Therefore the environments inferred from this fauna are not different from those in the present day.

6. Tanuki-ana Cave

The mammalian remains obtained from this cave are assigned to 29 forms (excluding *Microtus* sp. indet.; Table 16). Of these, only one form is possibly extinct (*Petaurista* sp.).

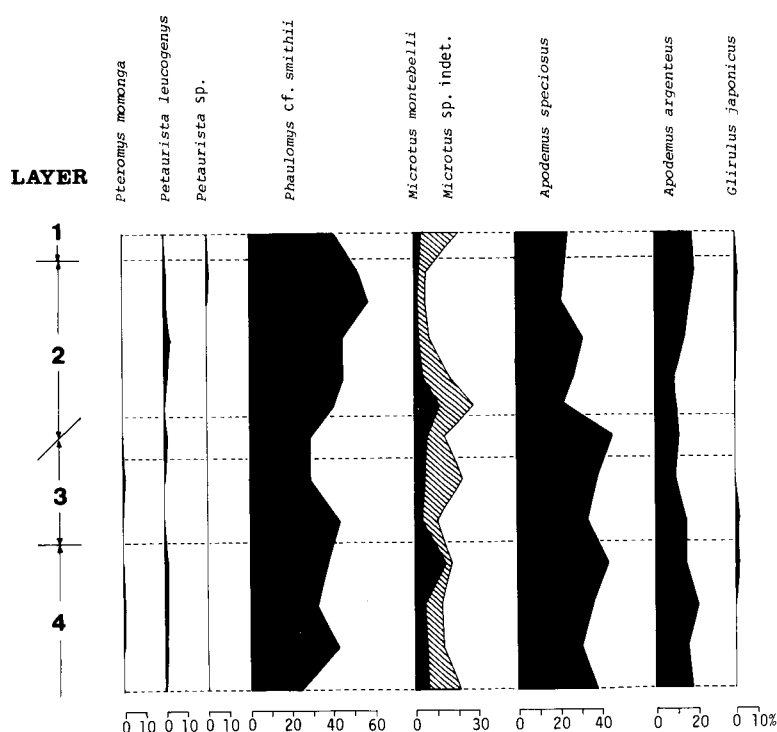


Fig. 69. Diagram showing the relative abundance of each form of rodents based on the total number of skull (mostly fragmental maxilla), mandible and isolated tooth in each horizon of the sediments of Tanuki-ana Cave.

Table 16. Stratigraphic distribution of the mammalian remains in the sediments of Tanuki-ana Cave. The total number of skull (mostly fragmental maxilla), mandible and isolated tooth is shown in each horizon. Moreover black circle (●) indicates the occurrence known from other parts.

LAYER	DEPTH	TAXON																																					
			INSECTIVORA	* <i>Sorex shinto</i>	<i>Crocidura dsinezumi</i>	* <i>Dymecodon pilirostris</i>	<i>Urotrichus talpoides</i>	<i>Euroscaptor mizura</i>	<i>Mogera</i> sp.	CHIROPTERA	<i>Rhinolophus cornutus</i>	<i>Rhinolophus ferrumequinum</i>	<i>Myotis macrodactylus</i>	<i>Miniopterus schreibersii</i>	<i>Murina leucogaster</i>	<i>Murina aurata</i>	LAGOMORPHA	<i>Lepus brachyurus</i>	RODENTIA	<i>Pteromys momonga</i>	<i>Petaurista leucogenys</i>	** <i>Petaurista</i> sp.	<i>Phaulomys</i> cf. <i>smithii</i>	<i>Microtus montebelli</i>	<i>Microtus</i> sp. indet.	<i>Apodemus speciosus</i>	<i>Apodemus argenteus</i>	<i>Glirulus japonicus</i>	CARNIVORA	<i>Nyctereutes procyonoides</i>	<i>Vulpes vulpes</i>	<i>Selenarctos thibetanus</i>	<i>Martes melampus</i>	<i>Mustela sibirica</i>	<i>Meles meles</i>	ARTIODACTYLA	<i>Sus scrofa</i>	<i>Cervus</i> sp.	
		exact horizon unknown	-	-	-	-	-	1		1	-	2	-	1	1	-	-	-	-	-	-	-	26	2	4	13	6	-	1	-	-	-	-	-	-	-	-	1	1
1	0-25 cm	-	-	-	-	-	-	●	-	-	-	-	1	-	-	-	-	-	-	-	-	-	58	4	25	34	21	-	2	-	-	-	-	-	1	-	1	-	
	25-40	-	-	-	-	●	●	●	-	-	-	-	-	-	-	-	-	-	-	1	1	99	2	7	42	34	2	2	-	-	-	-	-	-	1	8	-		
	40-50	-	-	-	5	●	16		3	5	4	-	3	1	2		2	-	2	-	133	3	8	48	38	1	24	-	-	2	1	5	-	-	-	-	-	1	1
2	50-75	-	1	-	1	-	8		1	3	1	-	2	3		1	-	7	-	130	6	15	92	41	1	9	-	-	-	-	-	-	-	-	-	-	-	8	8
	75-90	1	1	-	2	-	6		2	4	2	-	3	-		1	-	1	-	35	3	11	21	7	-	6	-	-	-	-	2	-	-	-	-	-	7	3	
	90-100	-	2	-	2	-	4	●	2	1	-	1	1		1	-	-	-	-	31	9	13	17	7	-	●	●	1	-	-	-	1	-	-	-	-	1	10	
	100-120	-	-	-	-	-	●	●	-	-	-	-	-	-	-	-	-	2	-	51	9	16	81	19	-	-	-	-	-	-	-	-	-	-	-	-	-	3	8
3	120-140	-	-	-	-	-	●	-	-	-	-	-	-	-	-	-	-	-	1	-	-	33	5	21	43	11	-	-	-	-	-	-	-	-	-	-	-	11	3
	140-160	-	-	-	●	-	●	-	-	-	-	-	-	-	-	-	-	-	-	-	-	69	5	11	50	22	1	-	-	-	-	-	-	-	-	-	-	6	2
	160-180	-	-	-	-	●	-	●	-	-	-	-	-	-	-	-	-	-	4	-	130	5	9	147	48	2	-	-	-	-	-	-	-	-	-	-	-	4	●
4	180-200	-	-	-	-	●	●	●	-	-	-	-	-	-	-	-	-	-	1	1	-	106	13	27	116	63	-	-	-	-	-	-	-	-	-	-	-	2	3
	200-220	-	-	●	●	-	●	-	-	-	-	-	-	-	-	-	-	-	1	-	141	17	29	100	44	-	-	-	-	-	-	-	-	-	-	-	-	1	1
	220-240	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	29	7	18	43	20	-	-	-	-	-	-	-	-	-	-	-	-	-

* exotic form to west Honshu. ** extinct form.

Although the investigation of the remains other than rodents is still insufficient in Layers 3 and 4, the fauna of this cave is described as follows:

Rodent fauna (Fig. 69) —

The rodents are rich in number as well as in variety. Namely eight forms are recognized. Among these, *Phaulomys* cf. *smithii* and *Apodemus speciosus* are predominant in all the layers. In comparison with these two forms, *Microtus* and *A. argenteus* are poor in number. Moreover other four forms are very rare. Especially, *Petaurista* sp. is represented by a single molar from the upper part of Layer 2.

Associated fauna —

The insectivores comprise six forms. Of these, *Mogera* sp. is most abundant. *Urotrichus talpoides* is next in abundance, which is followed by *Crocidura dsinezumi*. In contrast with the abundant occurrence of these lowland forms, the high-mountain forms such as *Sorex shinto*, *Dymecodon pilirostris* and *Eurosaptor mizura* are rarely found in the insectivore assemblage. The chiropterans are composed of six forms. Of these, *Rhinolophus ferrumequinum* is most abundant. The lagomorphs are exclusively represented by *Lepus brachyurus*, which is uncommonly found.

The carnivore remains are assigned to six species. Of these, *Nyctereutes procyonoides* is most abundant, while *Meles meles* is next in abundance. The remaining four species are scarce. The artiodactyls are composed of *Sus scrofa* and *Cervus* sp. The former species is more abundant than the latter in most horizons.

General remarks —

The ratio of extinct forms plus exotic forms to Japan is evaluated as 3% in all taxa and 0% in other orders than rodents. These values are near to those in the Holocene localities such as Horizon I of Kannondo Cave Site and Domen Cave Site, but much lower than those in the Late Pleistocene localities such as F₄ of Kumaishi-do Cave and Horizons M to P of Kannondo Cave Site.

Excepting the rare occurrence of the high-mountain forms and extinct form, the fauna of this cave is fundamentally identical with that of the present west Honshu. Therefore it is assumed that the vegetational and climatic conditions were nearly equal to those in the present day, when the fossiliferous sediments of this cave were deposited.

7. Husen-ana Cave

The mammalian remains are assigned to 13 forms (excluding *Microtus* sp. indet.) which contain neither extinct nor exotic forms (Table 6).

Rodent fauna —

Four forms of rodents are recognized in the assemblage of this cave. Among these, *Phaulomys* cf. *smithii* is highly predominant. *Apodemus speciosus* is much fewer than this form, but considerably exceeds *A. argenteus* in number. On the other hand, *Microtus* is very rare.

Associated fauna —

The insectivores are composed of four forms which contain no high-mountain forms. Of these four, *Mogera* sp. B is most abundant, which is followed by *Crocidura dsinezumi*, *Urotrichus talpoides* and *M.* sp. A in order of abundance. The carnivore remains are very rare, but are

assigned to three forms.

General remarks —

Although the fauna of this cave is poorer than that of Tanuki-ana Cave in variety and number of material, the composition of the former is essentially identical with that of the latter. Moreover the fauna of this cave bears a strong resemblance to that of the present west Honshu. Therefore it suggests the similar environments to those in the present day.

8. Hirao-ana Cave and Ohera-ana Cave

The fossil assemblage of Hirao-ana Cave is poor in variety and abundance. Only four species of mammals are recognized, which include neither extinct nor exotic forms (Tables 9, 10). The rodents are not represented in these tables, but SOTSUKA (1972a) reported an indeterminate rodent specimen from this cave.

The assemblage of Ohera-ana Cave is richer than that of Hirao-ana Cave not only in variety but also in abundance (Tables 9, 10). It comprises eight forms of mammals (excluding *Microtus* sp. indet.) which contain neither extinct nor exotic forms. In these mammals, the rodents are restricted to *Microtus montebelli* and *Apodemus speciosus*.

9. Ninjinkubo First Cave

Twenty forms of mammals are recognized in the assemblage of this cave (Tables 9, 10). All of them are extant. The relative abundance of micro-mammals in this assemblage is diagrammatically shown in Fig. 70.

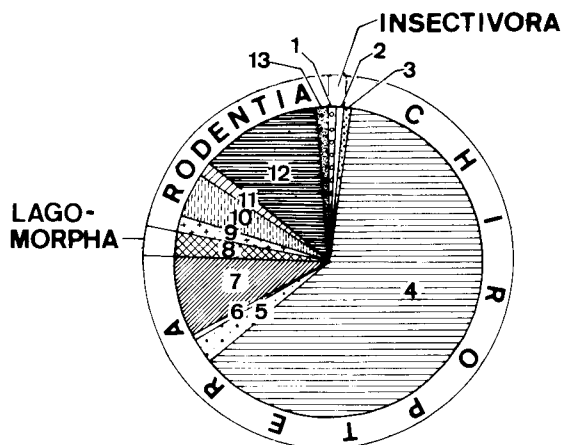


Fig. 70. Composition of the micro-mammalian remains obtained from Ninjinkubo First Cave. The ratio of the number of mandibles is shown (total = 189).

1, *Crociodura dsinezumi*; 2, *Urotrichus talpoides*; 3, *Rhinolophus cornutus*; 4, *R. ferrumequinum*; 5, *Myotis macrodactylus*; 6, ? *Miniopterus schreibersii*; 7, *Murina leucogaster*; 8, *Lepus brachyurus*; 9, *Petaurista leucogenys*; 10, *Phaulomys* cf. *smithii*; 11, *Apodemus speciosus*; 12, *A. argenteus*; 13, *Myomorpha*, fam., gen. et sp. indet.

Rodent fauna —

The rodents are composed of four forms, in which *Apodemus argenteus* is most abundant. This species is followed by *Phaulomys* cf. *smithii*, *A. speciosus* and *Petaurista leucogenys* in order of abundance.

Associated fauna —

The insectivores are scarcely found, and composed of four forms. The chiropterans are highly predominant in this assemblage, and comprise five species. Of these, *Rhinolophus ferrumequinum* is most abundant, while *Murina leucogaster* is next in abundance. However the remaining three species are rare.

The primates are represented by *Macaca fuscata* and *Homo sapiens*. The occurrence of the latter is cited from SOTSUKA *et al.* (1982), who regarded it as the man of the Jomon Period. The lagomorphs and carnivores comprise one and two forms respectively. On the other hand, the artiodactyl remains are exclusively assigned to *Sus scrofa* and *Cervus nippon*.

General remarks —

This fossil assemblage is characterized by the predominance of the chiropterans. They possibly roosted this cave, and their remains accumulated on the cave floor. Because this cave is a deep vertical cave as shown in Chapter IV, it possibly acts a pitfall trap. It is inferred that the mammals other than the chiropterans fell down from the entrance.

The ratio of extinct forms plus exotic forms to Japan is 0% in all taxa as well as in other orders than rodents. The faunal composition is identical with that of the present day. Therefore it is assumed that the environments were equal to those in the present day, when this assemblage was formed.

10. Yakubono-ana Cave

The mammalian remains obtained from this cave are poor in number, but are assigned to six forms which include two rodent forms such as *Phaulomys* cf. *smithii* and *Apodemus argenteus* (Tables 9, 10). All of these forms are extant.

11. Ojika-do Cave (Tables 9, 10)

Few mammalian remains from Chamber 1 are examined in the present study. They are assigned to *Petaurista leucogenys*, *Phaulomys* cf. *smithii* and *Nyctereutes procyonoides*. In addition to these, HASEGAWA *et al.* (1968) listed ten forms from this chamber.

From Chamber 2, HASEGAWA *et al.* (1968) reported a unique assemblage which was composed of *Macaca fuscata* and *Homo sapiens* only. However the present study reveals that five forms of mammals can be added to the fauna of this chamber. *P.* cf. *smithii* is the only representative of rodents in these five.

The sediments of Branch 1 yield 14 forms of mammals which include four forms of rodents. In the rodent assemblage, *A. argenteus* is most abundant, and *P.* cf. *smithii* is next in abundance. The remaining two are much fewer than *P.* cf. *smithii*.

The mammalian faunas of these three sites contain neither extinct nor exotic forms. They are similar to the fauna of Ninjinkubo First Cave as well as that of the present west Japan.

12. Oiwa-ana Cave

10 forms of mammals are obtained from this cave (Tables 9, 10). The micro-mammals are restricted to the rodents and lagomorphs which comprise five living forms. Of these five, *Phaulomys* cf. *smithii* is most abundant. The middle- and large-sized mammals are composed of two carnivore and three artiodactyl living species. The occurrence of a domestic species, *Capra hircus*, suggests that the present assemblage is very recent in age.

13. Yoshigatani Third Cave

As shown in Tables 9 and 10, the mammalian remains of this cave are assigned to eight forms. In these remains, the rodents are scarcely found, but comprise three forms (*Phaulomys* cf. *smithii*, *Apodemus speciosus* and *A. argenteus*). The remaining materials are not abundant, and are referred to one chiropteran, one primate, two carnivore and one artiodactyl species.

The fauna of this cave contains neither extinct nor exotic forms, because "*Sus nipponicus*" is presumably synonymized with a living species, *Sus scrofa* (see p. 101).

VI. Chronology and Correlation

The chronological data obtained by the non-faunal methods are summarily shown in Table 17. Based on these data as well as the stratigraphic and faunal descriptions given in Chapters IV and V, the geological age of the sediments of each locality is estimated. In this chapter, the grounds for the dating are discussed in each locality, and the chronological relationships among the localities are determined.

A. Middle Pleistocene localities

The chronological data are most abundantly obtained from the sediments of Locality 3 of Ube Kosan Quarry. The age of travertine from Layer 3 is determined as $192,000^{+44,000}_{-30,000}$ yr. B.P. by the U-series method, and bone fragments from Layer 4 are dated as earlier than $137,000^{+9000}_{-8000}$ or $143,000 \pm 9000$ yr. B.P. by the same method. The amino-acid date of bone fragments from Layer 17 is calculated as ca. 150,000 yr. B.P., when the rate constant (k) is evaluated as $3.84 \times 10^{-6} \text{ yr}^{-1}$, which is obtained from the calibration samples from Kannondo Cave Site. These data indicate that the sediments of this locality are assigned to the later stage of the Middle Pleistocene. On the other hand, the fluorine contents of fossil bones are analysed in each layers, but no significant differences can be detected among these layers. In contrast to this, the uranium contents increase in accordance with the stratigraphic sequence of the sediments.

As already mentioned in Chapter IV, Layer 1 of Locality 1 of the same quarry is stratigraphically correlative with the lowest layer (Layers 1 to 4) of Locality 3. Therefore Layers 2 to 4 of the former locality is somewhat older than the lowest layers of the latter locality. Such correlation is consistent with the fluorine contents of fossil bones in both localities (Table 17).

Table 17. Chronological data of the cave and fissure sediments examined in the present study. As regards the fluorine content, mean, standard deviation and number of examined specimens (N) are shown. * Layer 4; ** Layers 2 to 4; *** this value includes the data from other layers of this locality.

LOCALITY	Radiocarbon date (yr. B.P.)	U-series date (yr. B.P.)	Amino-acid date (yr.B.P.)	Uranium content in fossil bone (ppm)	Fluorine content in fossil bone (%)	Tephro-chronology (yr.B.P.)
Aisawa Quarry	—	—	—	—	—	> 32000±4000 or >31000±8000
Kumaishi-do Cave						
F ₄	16720±880	—	—	—	0.795±0.236 (N=13)	—
F ₅	—	—	—	—	1.29±0.20 (N=4)	—
Sugi-ana Cave						
light coloured bone	—	—	—	—	1.19±0.28 (N=3)	—
dark coloured bone	—	—	50000	—	—	—
very dark coloured bone	—	—	137000	—	1.78±0.49 (N=3)	—
Yage Quarry						
Site 3	—	—	—	—	2.57±0.15 (N=2)	—
Site 4-d	—	—	—	—	1.37±0.25 (N=3)	—
Site 5	18040±990	—	—	—	1.87±0.52 (N=3)	—
Suse Quarry						
East Fissure	14710±670	—	—	—	1.05±0.17 (N=10)	—
West Fissure	—	—	—	—	0.92±0.07 (N=7)	—
Kannondo Cave Site						
Horizon I	—	—	—	—	0.200±0.125 (N=8)	—
Horizons J to L	—	—	—	—	0.480±0.127 (N=13)	—
Horizon M (lower)	—	—	—	—	—	16000±400
Horizon N	20150±300	—	—	—	0.489±0.138 (N=7)	21000-22000
Horizon O (upper)	—	—	31900	—	0.665±0.153 (N=11)	—
Tanuki-ana Cave	7580±250*	—	—	—	0.339±0.073 (N=5)**	—
Loc.1 of Ube Kosan Quarry (Layer 2)	—	—	—	—	1.08±0.23 (N=6)	—
Loc.2 of Ube Kosan Quarry	—	—	—	—	—	> ca.70000
Loc.3 of Ube Kosan Quarry						
Layer 17	—	—	150000	9.8	0.866±0.187 (N=22)***	—
Layer 4	—	>137000 ⁺⁹⁰⁰⁰ ₋₈₀₀₀ or >143000±9000	—	14.3 19.6		—
Layer 3	—	192000 ⁺⁴⁴⁰⁰⁰ ₋₃₀₀₀₀	—	—		—
Ikumo Quarry	—	>184000 ⁺¹⁴⁰⁰⁰ ₋₁₃₀₀₀	—	34.3	1.06	—
Ando Quarry	—	—	—	—	1.04±0.348 (N=5)	—
Sumitomo Quarry	—	>174000±22000	—	—	—	—

No materials suitable for the physical and chemical dating are available from the sediments of Locality 4 of Ube Kosan Quarry. The sediments of this locality are tentatively correlated with those of Locality 1 of the same quarry by the characters of the associated fauna.

By the U-series dating method, fossil bones from Ikumo Quarry are dated as earlier than $184,000^{+14,000}_{-13,000}$ yr. B.P. Although their fluorine contents are only slightly higher than those of Locality 3 of Ube Kosan Quarry, their uranium content is much higher than those of the latter locality. Because it can be regarded that the usage of the uranium content provides better results than that of the fluorine content in the dating of older fossil bones, it is assumed that the sediments of Ikumo Quarry are considerably older than those of Locality 3 of Ube Kosan Quarry. This inference is supported by the ratios of extinct forms plus exotic forms to Japan in the associated faunas of both localities. Namely the ratio is about 43% in Ikumo Quarry, which far exceeds the value in Locality 3 (about 21%).

Ando Quarry is one of the most important Middle Pleistocene localities in Japan (Fig. 4), although the fossil materials from this locality are not described in this paper. These materials were already studied by HASEGAWA (1966), KOWALSKI and HASEGAWA (1976), HASEGAWA *et al.* (1977) and HACHIYA *et al.* (1985). As shown in Table 17, fossil bones from Ando Quarry show similar fluorine contents to those from Ikumo Quarry as well as to those from Locality 1 of Ube Kosan Quarry. The ratio of extinct forms plus exotic forms to Japan calculated from the data of the above-mentioned references is about 39% in the associated fauna, which is very near to the value in Ikumo Quarry. On the other hand, the ratio is much higher than those in Localities 1 and 3 of Ube Kosan Quarry. Therefore it is inferred that the sediments of Ando Quarry is roughly contemporaneous with those of Ikumo Quarry.

Fragments of travertine from Sumitomo Quarry are dated as earlier than $174,000 \pm 22,000$ yr. B.P. by the U-series dating method. However the ratio of extinct forms plus exotic forms to Japan is higher in this quarry (50.0%) than in Ikumo Quarry. Consequently it is assumed that the sediments of Sumitomo Quarry is somewhat older than those of Ikumo Quarry.

B. Late Pleistocene localities

As already described in Chapter IV, the fossiliferous sediments of Aisawa Quarry are assignable to the Upper Kuzuu Formation. According to SHIKAMA (1949), this formation is overlain by the breccia bed with a thickness of 10 m. Moreover the latter bed is covered by the Kanuma Pumice Bed with the fission track age of $32,000 \pm 4000$ or $31,000 \pm 8000$ yr. B.P. Because it is assumed that somewhat long duration was interposed between the deposition of this pumice bed and that of the Upper Kuzuu Formation, the age of the latter can be estimated as the early stage of the Late Pleistocene.

The stratigraphic sequence of the Nojiri-ko Formation is well investigated, and a number of ^{14}C dates are obtained from its various horizons (see Chapter IV). These data clearly indicate that this formation is assigned to the later stage of the Late Pleistocene.

Fossil bones obtained from Layers 4 and 5 of F₄ of Kumaishi-do Cave are dated as $16,720 \pm 880$ yr. B.P. by the ^{14}C method. Because the fluorine contents in fossil bones from each layer show no significant differences, the overall sediments of F₄ are assignable to the latest

part of the Late Pleistocene. On the other hand, fossil bones from F_3 of the same cave have higher fluorine contents than those from F_4 (Table 17). Therefore the sediments of F_3 are considered to be older than those of F_4 . Such an inference on their time relationship is supported by the fact that *Anourosorex japonicus* is rarely found in F_3 , whereas it is completely absent from F_4 .

Fossil bones from Sugi-ana Cave show a wide range of variation in colour as well as in degree of fossilization. The fluorine contents of light-coloured and less-fossilized bones are considerably lower than those of dark-coloured and well-fossilized bones. An amino-acid date of the former bones is determined as about 50,000 yr. B.P., when the fossil bones from F_4 are used as calibration samples. On the other hand, the latter bones are dated as about 137,000 yr. B.P. by the same method. Therefore the sediments of this cave are mostly assigned to the early stage of the Late Pleistocene.

The geological ages of the sediments at six sites of Yage Quarry are summarily given in Chapter IV (p. 69). The sediments of Sites 2, 4 (4-a to 4-e) and 5 as well as the uppermost part of the sediments of Site 1 are considered to be of Late Pleistocene age. The reasons for such age estimation are summarized as follows:

1. Fossil bones from Site 5 are dated as $18,040 \pm 990$ yr. B.P. by the ^{14}C method (GaK-11494).
2. The ratio of extinct forms plus exotic forms to Japan in the associated fauna is calculated as about 15% in Site 5. This value is much lower than those in the Middle Pleistocene localities but much higher than those of the Holocene localities.
3. The fluorine contents of fossil bones from Sites 4-d and 5 are higher than those in the Holocene localities near this quarry.
4. The sediments of Sites 5 and 4-d are similar to those of Sites 2, 4-a, 4-b, 4-c and 4-e as well as of the uppermost part of Site 1. Moreover there are no fundamental differences in the composition of the associated fauna among these sites. Therefore these sediments are roughly correlative with each other.
5. The sediments of these sites yield no remains of *Sus scrofa*, but yield exotic and extinct forms in the associated fauna including *Anourosorex japonicus*, *Ursus arctos*, *Panthera tigris*, *Cervus praenipponicus* and *Sinomegaceros yabei*.

In addition to these, the extinct and exotic forms of carnivores and artiodactyls known from the Upper Kuzuü Formation are mostly lacking (for example, *Mustela kuzuensis*, *Martes ten*, *Meles leucurus kuzuensis* and *Moschus moschiferus*). Taking this character into consideration, the age of these sediments seems to be restricted to the later stage of the Late Pleistocene.

Because the ^{14}C age of fossil bones from East Fissure of Suse Quarry is determined as $14,710 \pm 670$ yr. B.P. (GaK-11495), the sediments of this fissure is undoubtedly dated as the later stage of the Late Pleistocene. Moreover the fluorine contents of these bones are higher than those of West Fissure of the same quarry.

As already mentioned in Chapter IV, the absolute dates of the Late Pleistocene horizons of Kannondo Cave Site are determined by various methods (Table 17). By means of tephrochronology, Horizon N and the lower part of Horizon M are dated as 21,000 to 22,000 yr. B.P. and about 16,000 yr. B.P. respectively. The calc tufa obtained from the former horizon is also dated as $20,150 \pm 330$ yr. B.P. by the ^{14}C method. Moreover MATSU'URA (1981) provided an amino acid date, 22,900 yr. B.P., for the upper part of Horizon O. However this value should be emended as 31,900 yr. B.P. by using a more reasonable rate constant (MATSU'URA, pers.

comm.). The age of the lowest horizon (Horizon P) is not determined by these methods. However, taking these chronological data and the thickness of the sediments of each layer into consideration, it is estimated as 50,000 yr. B.P. or more. Therefore it can be stressed that the sediments of the Late Pleistocene horizons represent almost all the periods of the later stage of the Late Pleistocene.

The fossiliferous sediments of Locality 2 of Ube Kosan Quarry are conformably overlain by the volcanic ash layer dated as ca. 70,000 yr. B.P. Therefore they are assigned to the early stage of the Late Pleistocene.

No chronological data by the physico-chemical methods are obtained from the fossiliferous sediments of Seiryukutsu Cave and Mejiro-do Cave. However the associated fauna of the former contains *Anourosorex japonicus* in low frequency as well as *Palaeoloxodon naumanni*, but lacks *Sus scrofa*. Therefore the geological age of the sediments of Seiryukutsu Cave is assumed to be of Late Pleistocene age. On the other hand, *Sinomegaceros* sp. is found in association with *S. scrofa* from the sediments of Mejiro-do Cave, but *A. japonicus* is absent. Moreover the fossil bones obtained from this cave are less fossilized than those from Seiryukutsu Cave. These facts suggest that the sediments of Mejiro-do are younger than those of Seiryukutsu Cave, and are assigned to the Latest Pleistocene.

The lowest layer of Minatogawa Site is dated as $18,250 \pm 650$ and $16,600 \pm 330$ yr. B.P. by the ^{14}C method, where *Sus* and cervids are coexistent. Therefore this layer is considered to be of Latest Pleistocene age. On the other hand, the coexistence of *Sus* and cervids is observed in Kuteken, Iso and Gajanbira. This indicates that the fossiliferous sediments of these localities are also assignable to the Latest Pleistocene.

C. Holocene localities

The fossiliferous sediments of West Fissure of Suse Quarry are considered to be of Early Holocene age. The reasons for such age estimation are summarized as follows:

1. The fluorine contents of fossil bones are significantly lower than those of East Fissure of the same Quarry.
2. The sediments yield abundant remains of *Sus scrofa*.
3. The associated fauna contains neither extinct nor exotic forms.

The sediments of Kitoragawa Site, Domen Cave Site, Anagami Rockshelter Site and the Holocene horizons of Kannondo Cave Site are well stratified and dated in detail by the archaeological method. They are undoubtedly assigned to Holocene. The relative ages of each cultural layer in each site are closely described in Chapter IV.

In Tanuki-ana Cave, the arrow heads of the Early Jomon Period were obtained from Layer 2, while the fossil bones collected from Layer 4 are dated as 7580 ± 250 yr. B.P. by the ^{14}C method (GaK-10734). Therefore the sediments hitherto excavated are undoubtedly assigned to Holocene. Such age estimation is well coincident with relatively low fluorine contents in fossil bones from Layers 2 to 4 (Table 17).

Fossil bones from Husen-ana Cave are generally less fossilized than those from Tanuki-ana Cave. Moreover the associated fauna contains neither extinct nor exotic forms. Therefore the

fossiliferous sediments of this cave are considered to be of Holocene age.

The mammalian remains from six caves on the Hirao-dai Plateau such as Hirao-ana Cave, Ohera-ana Cave, Ninjinkubo First Cave, Yakubono-ana Cave, Ojika-do Cave and Oiwa-ana Cave are considered to be Holocene in age from the following reasons:

1. The remains were collected from the superficial sediments on the cave floor just below each cave entrance, and are almost unfossilized.
2. Neither extinct nor exotic forms are found in the associated fauna (excluding the forms which were extinguished very recently).
3. *Sus scrofa* commonly occurs in the associated fauna of these caves except Hirao-ana Cave and Ohera-ana Cave.

Fossil bones from Yoshigatani Third Cave are somewhat more fossilized than those from these six caves. However the associated fauna of this cave contains neither extinct nor exotic forms. Moreover *Sus scrofa* is recognized in the fauna. These facts suggest that the fossiliferous sediments of this cave are also Holocene in age.

D. Correlation and chronological subdivision

Summarizing up the above-mentioned discussions, the chronological relationship among the fossil localities are diagrammatically shown in Fig. 71. This figure indicates that the fossiliferous sediments of these localities cover the period from the middle stage of the Middle Pleistocene to Holocene. In order to describe the succession of the rodent fauna, this period is tentatively divided into the following five stages:

Stage	Absolute age of lower boundary (yr. B.P.)
A. Holocene	ca. 10,000
B. late Late Pleistocene	50,000 to 70,000
C. early Late Pleistocene	ca. 130,000
D. late Middle Pleistocene	? 250,000 to 300,000
E. middle Middle Pleistocene	

Although the ages of the boundaries between Holocene and the Late Pleistocene and between the Late and Middle Pleistocene are generally accepted, those of other boundaries are tentative. All the fossil localities examined in this paper can be referred to these five stages (see Fig. 71).

- A: All the Holocene localities described in Chapter IV.
- B: Nojiri-ko Formation; F₃ and F₄ 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: Aisawa Quarry (Upper Kuzuü Formation); Sugi-ana Cave (mostly); Locality 2 of Ube Kosan Quarry.
- D: Localities 1, 3 and 4 of Ube Kosan Quarry.
- E: Ikumo Quarry; Sumitomo Quarry; Ando Quarry.

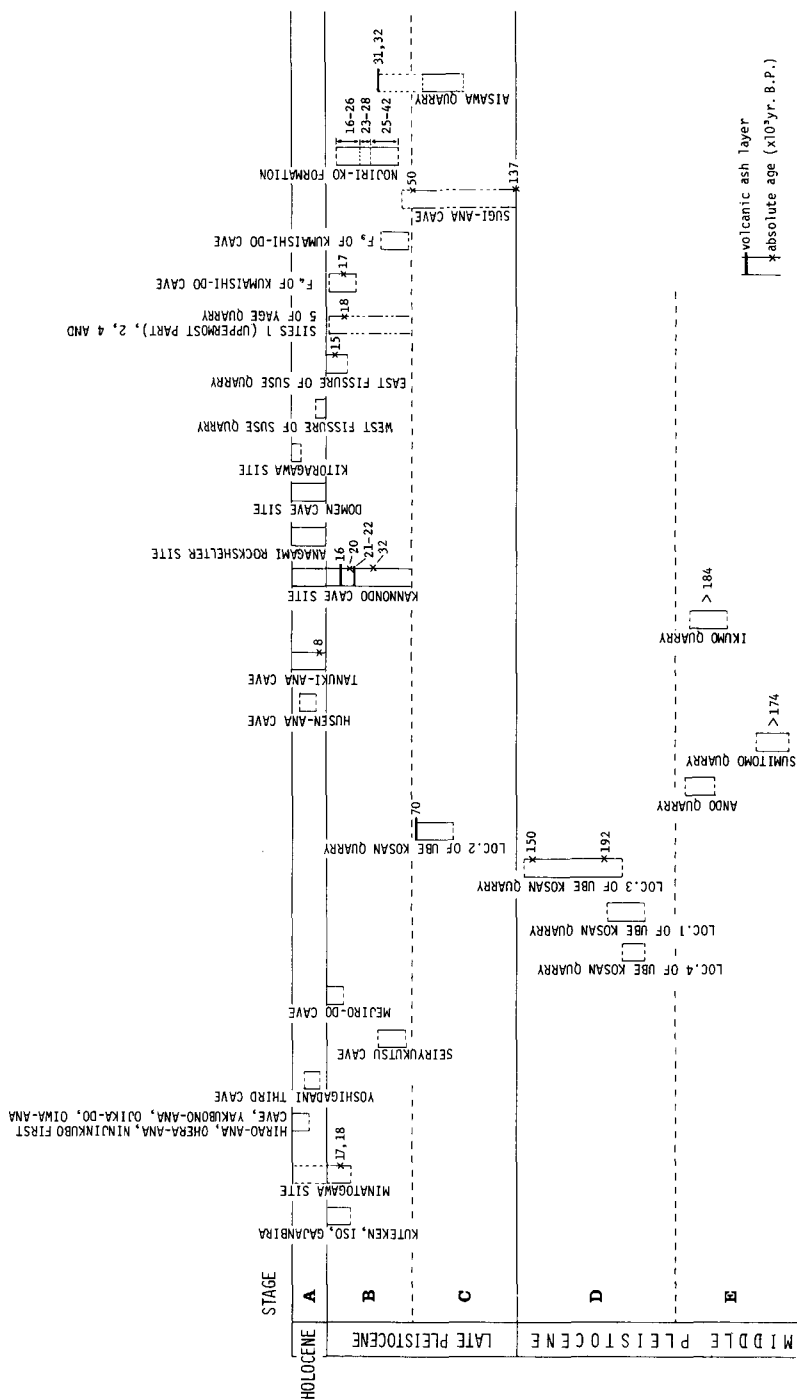


Fig. 71. Correlation chart showing the chronological relationship among the fossil localities.

VII. Systematics

A. Method of measurements and terminology

1. Method of measurements

All measurements were taken with a profile projector (Nikon V-12) with an electric digital counter (Nikon CM-65), and recorded to the nearest 0.001 mm. Because the last figure is less significant, it is rounded up in the subsequent tables of the measurements.

The fossil materials examined here are composed mainly of mandibles and isolated cheek teeth. Therefore the method of measurements for these parts are exclusively described below.

Mandible —

The measuring points are defined as follows:

Coronion (cr): The highest point of the coronoid process. This point is, however, mostly missing in the fossil mandibles of rodents.

Gonion caudale (goc): The most posterior point of the angular process.

Gonion ventrale (gov): The most basal point of the angular process.

Infradentale (id): The most anterior point of the horizontal ramus.

The following 18 measurements are carried out in the present paper (Fig. 72; numbers given below correspond to those in the figure).

1. Total length of the mandible: *id* to *goc*.
2. Ditto: *id* to the most posterior point of the condyle.
3. Length from the anterior tip of the incisor to the most posterior point of the condyle.
4. Length of the horizontal ramus: *id* to the posterior border of the alveolus of M_3 .
5. Length of the diastema: *id* to the anterior border of the alveolus of M_1 .
6. Length of the ascending ramus: The posterior border of the alveolus of M_3 to the most posterior point of the condyle.
7. Ditto: The posterior border of the alveolus of M_3 to *goc*.
8. Height of the ascending ramus: *gov* to the highest point of the condylar process. Measured at right angles to the tangent line of the basal margin at *gov*.
9. Ditto: *cr* to the uppermost point of the lower border of the ascending ramus.
10. Ditto: *gov* to the deepest point of the mandibular incision.
11. Length of the mandibular incision: *cr* to the most posterior point of the condyle.
12. Height of the horizontal ramus at M_1 (in arviculids, murids and glirids) or at P_4 (only in sciurids): Measured along the lingual side at right angles with the alveolar line. In arviculids, the maximum height is measured (compare A with C in Fig. 72).
13. Minimum height of the horizontal ramus (in sciurids, arviculids and glirids), or height of the horizontal ramus at M_3 (in murids): Measured along the lingual side. In murids, it is measured at right angles with the tangent line of the basal margin at its highest point (Fig. 72, C).
14. Maximum thickness of the horizontal ramus: Measured at right angles with the long axis of the ramus.
15. Length of the cheek tooth row (P_4 to M_3 in sciurids and glirids; M_1 to M_3 in arviculids and murids) at the occlusal level (in arviculids) or at the crowns (in other families).
16. Ditto at the alveoli.
17. Length of the molar row (M_1 to M_2) at the occlusal level (in arviculids) or at the crowns (in other families).
18. Ditto at the alveoli.

Cheek teeth —

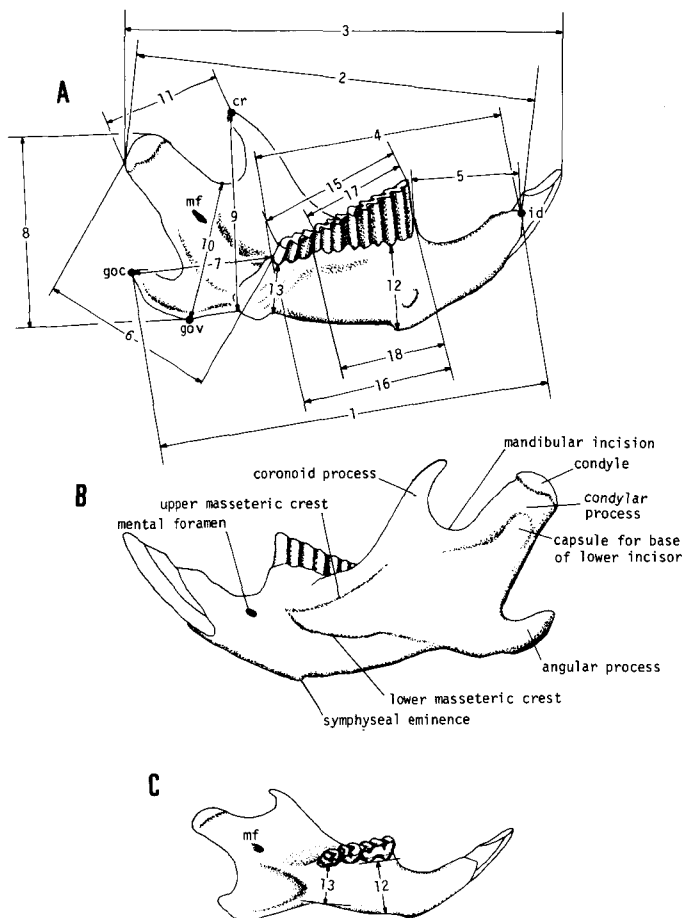


Fig. 72. Method of measurements and terminology for rodent mandibles. A, B, mandible of arvicolids (A, lingual view; B, buccal view); C, mandible of murids (lingual view). cr, coronion; goc, gonion caudale; gov, gonion ventrale; id, infradentale; mf, mandibular foramen; 1-18, measurements adopted here (for detailed explanation see text; these numbers correspond to those in text).

In sciurids, murids and glirids, the maximum length and width of the crown are measured (Figs. 73, 74, 77, 78). Excessively or abnormally worn specimens are excluded from the present measurements. In arvicolids, the maximum length and width of the occlusal surface are measured (Fig. 76). Because these dimensions are much smaller in young individuals than in grown ones (Fig. 112), the data of the former individuals (the age-class Y in *Clethrionomys* and *Phaulomys* and its correlatives in the other arvicolids; see p. 208) are excluded from the subsequent tables of the measurements.

In all the cases, the length is measured along the long axis of the crown, while the width is measured at right angles with this axis.

2. Terminology

The terminology of rodent mandibles is given in Fig. 72. Because the morphology of their cheek teeth is variable in each group, the detailed explanations of the terminology are given in each family.

Sciuridae —

Among the sciurids, sciurines are considerably different from petauristines in the patterns of cheek teeth. Therefore the terminology of the cheek teeth of these two groups are given separately (Figs. 73, 74).

The cheek teeth of the sciurines are primitive, while those of the petauristines are highly modified (especially in the lower cheek teeth of *Petaurista*). The upper cheek teeth of the sciurines are characterized by four transverse lophs and one longitudinal loph (*endoloph*). Among these lophs, three transverse valleys are observed. The anterior and middle valleys correspond to the paraflexus and posterobuccal flexus of the petauristines respectively. The posterior valley is equivalent to the posterolingual diagonal flexus and postfossette of the latter group. Namely it is not differentiated into these two parts in the sciurines. The lower cheek teeth of the sciurines are morphologically very simple. Their crown comprises a central basin and surrounding marginal crests. In the primitive member of the petauristines (*Pteromys*), such a structure is fundamentally retained, but the crest on the buccal part of the crown is developed to form a high continuous ridge (*ectolophid*). In the advanced member (*Petaurista*), the central basin is divided into several parts by many transverse and diagonal ridges.

The terminology of the sciurine cheek teeth adopted here is based mainly on STEHLIN and SCHAUB (1951). On the other hand, that of the petauristine cheek teeth was described by DEHM (1962), McKENNA (1962), KOENIGSWALD (1973) and DAAMS (1977). Among these, McKENNA's terminology is mainly employed in the present paper, because it contains detailed

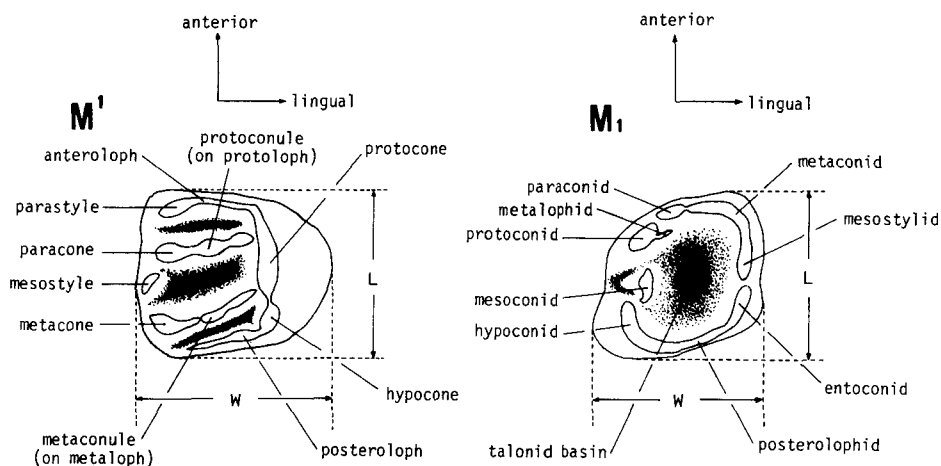


Fig. 73. Terminology and method of measurements for sciurine cheek teeth. L, length of crown; W, width of crown.

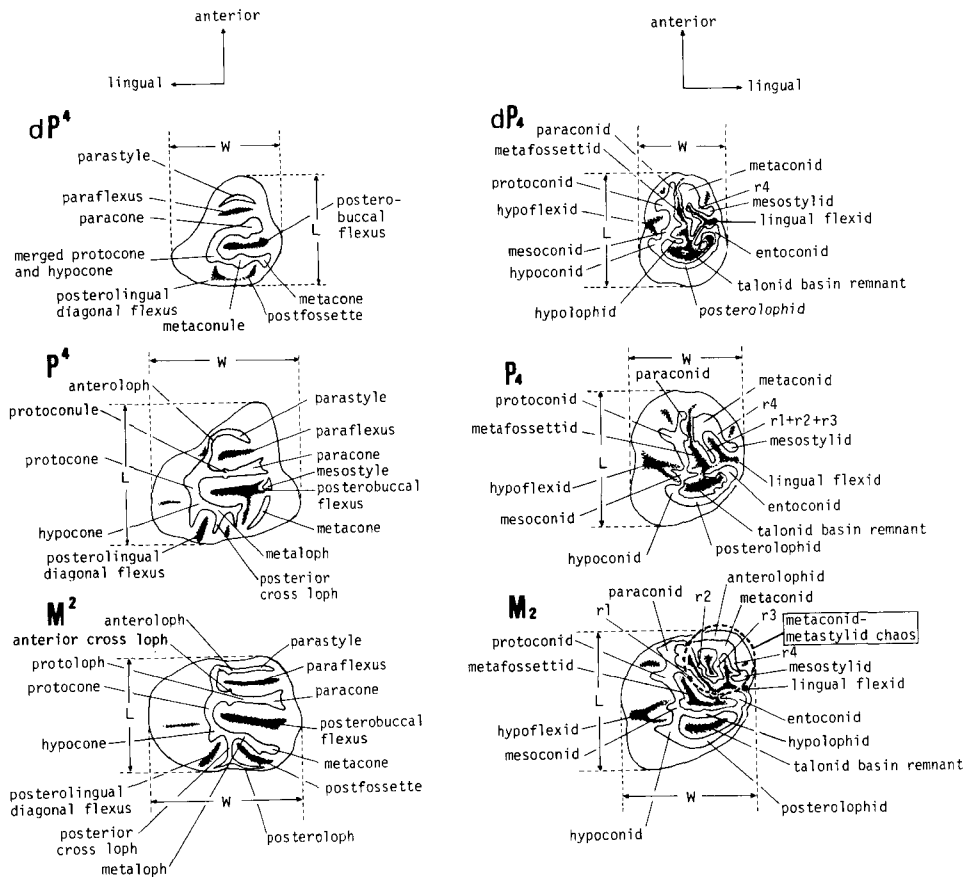


Fig. 74. Terminology and method of measurements for the petauristine cheek teeth. The terminology is mainly based on McKENNA (1962) and DEHM (1962). Ridges which were not named by them are tentatively called r1 to r4 here. L, length of crown; W, width of crown.

nomenclature of cusps, lophs and valleys. In addition to this, DEHM's one is partly cited.

Arvicolidae —

Arvicolids have tall prismatic molars whose occlusal surfaces show a characteristic pattern. This pattern is produced by several alternating triangles and one or two loops. The internal parts of these triangles and loops are formed by dentine, while they are surrounded by enamel bands. The apex of each triangle or loop, and the valley between neighbouring triangles or between a triangle and loop are called "salient angle" and "re-entrant angle" respectively.

In order to describe these molars, several systems of terminology have been proposed. They can be summarized as follows:

1) RÖRIG and BÖRNER's system: RÖRIG and BÖRNER (1905) denoted the dentine fields with numbers, and the inner and outer halves of each field (=lingual and buccal triangles) with alphabetical and greek small letters respectively. They also proposed formulae for the dentine fields and re-entrant folds of each molar. This system was followed fundamentally by OGNEV (1950). However he considera-

bly modified it, and added the numbering of the closed enamel fields.

2) HINTON's system: HINTON (1926) briefly explained the enumeration of the salient angles and re-entrant angles, and the naming of the other parts of the crown. Based mainly on this system, HIBBARD (1950) offered a more detailed nomenclature. In his enumeration system, the triangles, salient angles and re-entrant angles are expressed by numbers (1, 2, 3...), capital letters (A, B, C...) and small letters (a, b, c...) respectively.

3) STEHLIN and SCHAUB's system: Taking the homology of cusps into consideration, STEHLIN and SCHAUB (1951) provided a terminology in accordance with the Cope-Osbornian system. This terminology was followed by NIETHAMMER and KRAPP (1982), where HINTON's system was also accepted.

4) HERSHKOVITZ's system: In describing the South American cricetine rodents, HERSHKOVITZ (1962) proposed a detailed terminology of the molars. In his system, the Cope-Osbornian system was adopted for the names of the cusps, while unique names were also used for the enamel folds. HERSHKOVITZ's system was applied to the molars of the arviculids by AIMI (1980).

5) VANDEBROEK's system: VANDEBROEK (1966) applied his own terminology to the arviculid molars. His naming of each cusp differs from the Cope-Osbornian system (epicone, eocone, distocone etc. instead of protocone, paracone, metacone etc.).

6) MEULEN's system: MEULEN (1973) proposed an enumeration system for the triangles, salient angles, re-entrant angles, and anterior and posterior loops. This system contains the cusp homology in each molar as shown in STEHLIN and SCHAUB (1951).

In the present paper, MEULEN's system is adopted for describing the triangles, salient angles and re-entrant angles (Fig. 75). Namely the triangles (T) are counted from front backwards in upper molars, and from behind forwards in lower molars. Because the cusp homology is taken into consideration, T1 is logically absent from M^2 and M^3 . The enumeration for the lingual salient angles (LSA), buccal salient angles (BSA), lingual re-entrant angles (LRA) and buccal re-entrant angles (BRA) is carried out in the same manner. In this case, LSA1 and LRA1 are also missing in M^2 and M^3 . In order to describe the isthmuses (Is), a new enumeration system is introduced here (Fig. 76), which corresponds to the numbering of the other components mentioned above. In addition to these, HERSHKOVITZ's system (AIMI's application to the arviculids in 1980) is partly used for describing the minor structures of the molars of "*Clethrionomys-Phaulomys* group" (p. 210; Fig. 98).

Muridae:

In murids, three and two longitudinal cusp rows are characteristically observed in upper and lower molars respectively. Each cusp is united transversely to form laminae or chevrons. Such a cusp pattern is demonstrated to be derived from that of cricetids.

MILLER (1912) presented a terminology of the upper molars of the murids, where cusps are enumerated as t1 to t9. Namely in M^1 , the cusps of the anterior lamina are designated from lingual to buccal sides (t1, t2 and t3), and those of the middle and posterior laminae are numbered in the same manner (t4, t5 and t6 in the former; t7, t8 and t9 in the latter). MILLER's system have been adopted by several authors. In 1951, STEHLIN and SCHAUB attempted to interpret the cusp homology of these teeth using the Cope-Osbornian system. In this work, t5, t6, t8 and t9 were replaced by protocone, paracone, pseudypocone and metacone respectively, whereas t1, t2, t3, t4 and t7 were retained as MILLER's system.

In 1966, VANDEBROEK proposed a peculiar terminology for the murid molars which was quite different from the Cope-Osbornian system. VANDEBROEK's system were utilized for the designation of the lower molars by MISONNE (1969). For the upper molars, MISONNE basically

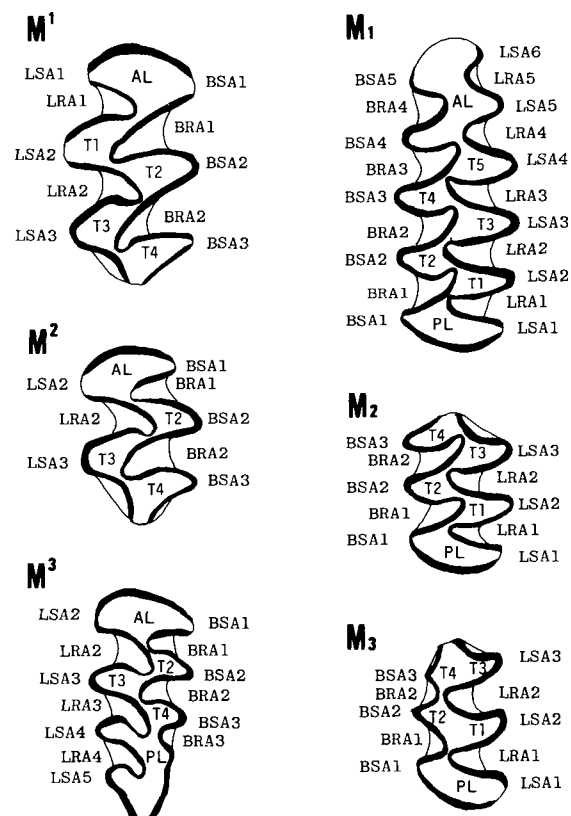


Fig. 75. Terminology of arvicolid molars (based mainly on MEULEN, 1973). AL, anterior loop; BRA, buccal re-entrant angle; BSA, buccal salient angle; LRA, lingual re-entrant angle; LSA, lingual salient angle; PL, posterior loop; T, triangle.

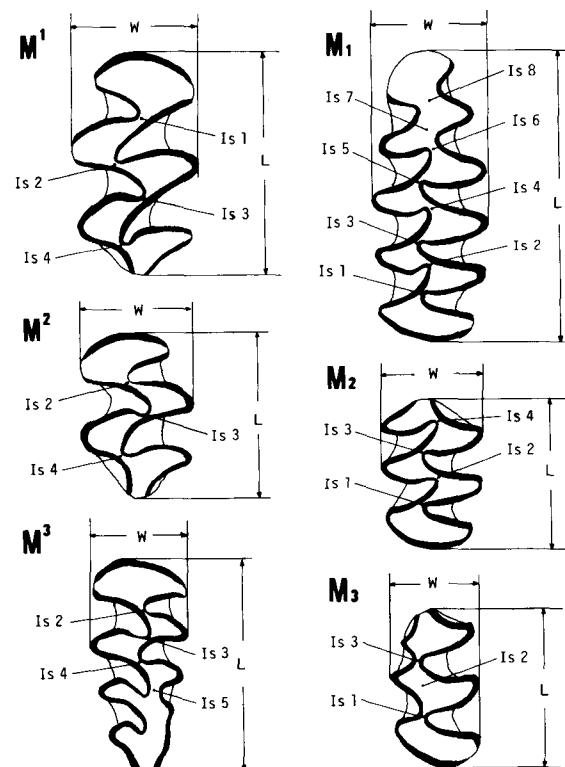


Fig. 76. Method of measurements and enumeration of isthmuses for arvicolid molars. L, length of occlusal surface; W, width of occlusal surface; Is, isthmus.

employed MILLER's nomenclature and added new names for a few minor elements (t1 bis, z and cc). MISONNE's terminology was followed by NIETHAMMER and KRAPP (1978).

In 1971, MICHAUX newly offered an enumeration system for the cusps of the lower molars, although his nomenclature for the upper molars was almost coincident with MISONNE's one (therefore basically with MILLER's system). Namely the main cusps of the lower molars are named tA, tB ... tF, and the antero-central and postero-central accessory cusps are also named tma and cp respectively. The accessory cusps on the buccal margin are numbered from

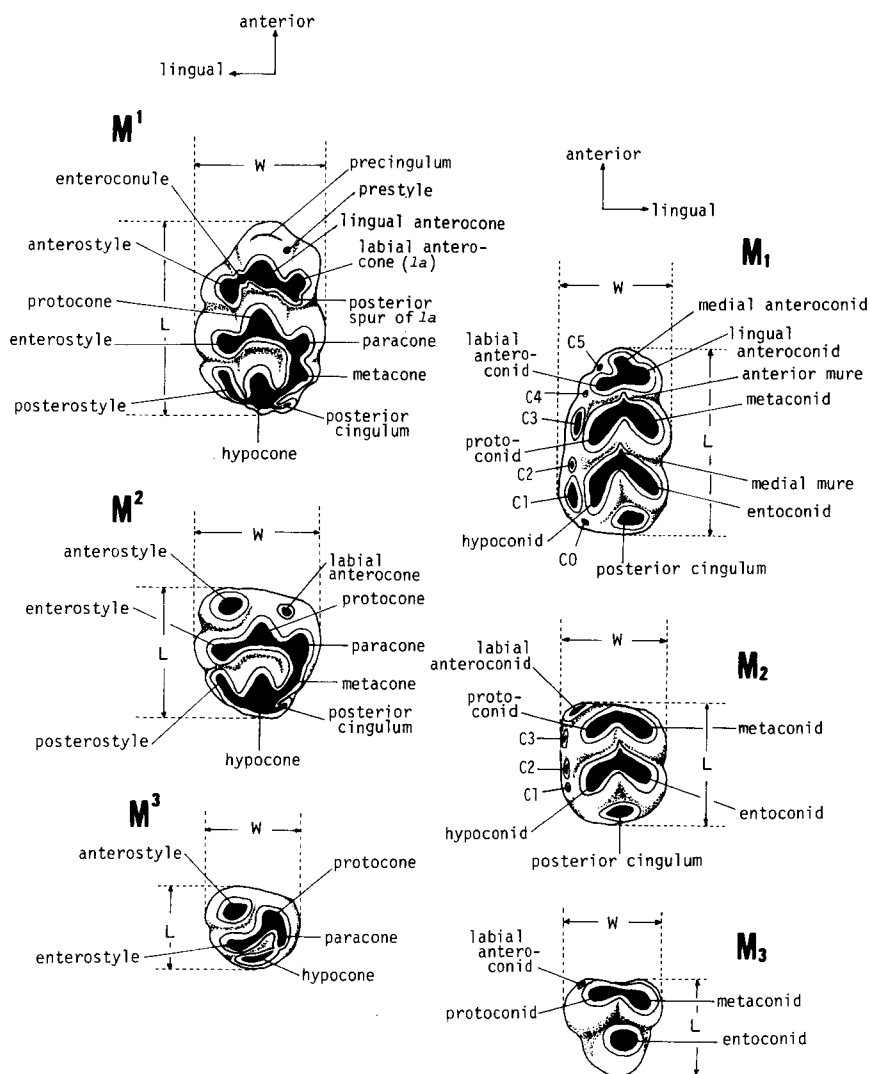


Fig. 77. Terminology and method of measurements for murid molars. The terminology is based mainly on JACOBS (1978). L, length of crown; W, width of crown.

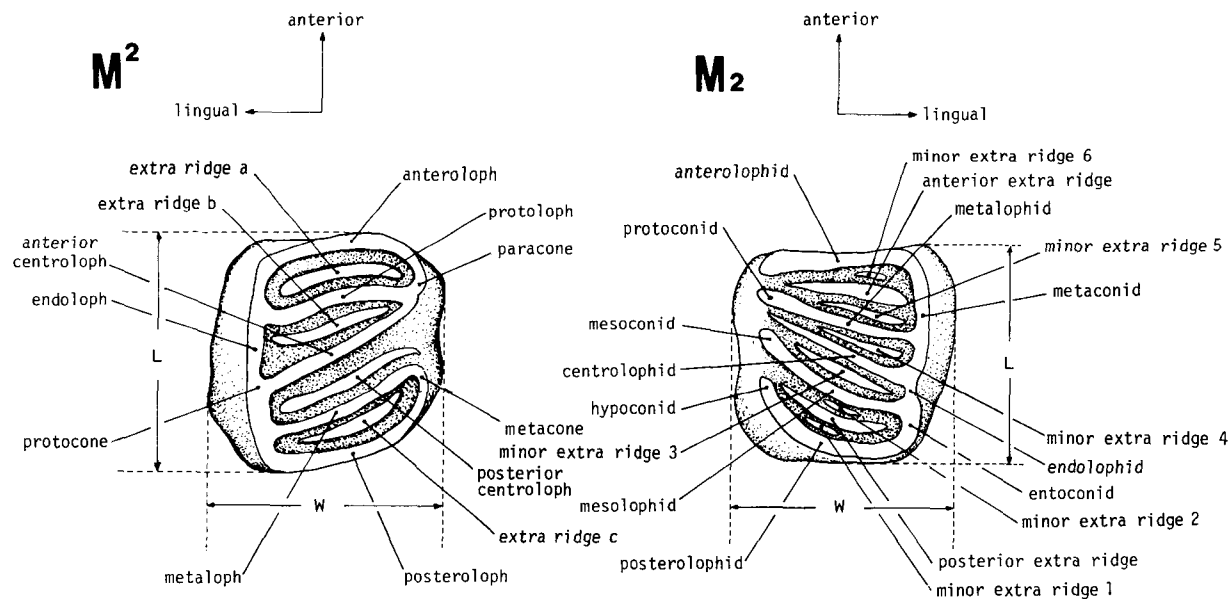


Fig. 78. Terminology and method of measurements for the glirid cheek teeth. The terminology is based mainly on BRUIJN (1966), but partly modified. L, length of crown; W, width of crown.

behind forwards as C1 to C5. This system was accepted by SEN (1977).

In 1974, JAMES and SLAUGHTER attempted to apply the Cope-Osbornian system to the lower molars, while they retained MILLER's t-nomenclature in the upper molars. WEERD (1976) and MUSSEY (1981a) adopted the same way of the designation of the cusps.

JACOBS (1978) reviewed the terminology of the previous authors, and discussed the relationship among them. Moreover he provided his own terminology which could be regarded as an adequate application of the Cope-Osbornian system not only to the upper molars but also to the lower molars (his Fig. 13). Because JACOBS' terminology is considered to be most consistent and convenient for describing the present materials, it is adopted here (Fig. 77).

Gliridae:

Glirids are characterized by low-crowned cheek teeth with many transverse ridges. Because the lophodont condition is highly advanced, it is very difficult to determine the cusp homology of these teeth in accordance with the Cope-Osbornian system. However several authors have attempted to give the terminology to them (STEHLIN and SCHAUB, 1951; VOLL-MAYR, 1966; BRUIJN, 1966 etc.).

The terminology used in this paper (Fig. 78) is based mainly on BRUIJN (1966). Because BRUIJN's terminology is insufficient for describing complicate types of the glirid molars, it is partly modified and several new names are introduced (extra ridges a, b and c of the upper cheek teeth, and minor extra ridges 1-6 of the lower cheek teeth).

Although some previous authors seem to have restricted the meaning of "endolophid" to a short ridge between metaconid and entoconid, "endolophid" in this paper means a longitudinal ridge on the lingual side of the crown as a whole including the metaconid and entoconid.

B. Systematic descriptions with identification keys

Five rodent families are known from the Quaternary sediments of the Japanese Islands. They are Sciuridae, Cricetidae, Arvicolidae, Muridae and Gliridae. All of these families except Cricetidae have also survived in the islands until the present day. By using the following key, they are easily distinguished from each other:

1. Size generally larger; postorbital process present; upper cheek teeth generally five in number, and with three or four transverse ridges on each crown; lower cheek teeth with a central basin and marginal ridges or with a very complicate pattern formed by a number of diagonal and transverse ridges. **Sciuridae**
- Size smaller; postorbital process absent; upper cheek teeth three or four; cheek teeth lacking the characters of Sciuridae mentioned above. 2
2. Four cheek teeth each on maxilla and mandible; these teeth extremely low-crowned, and with many fine transverse ridges. **Gliridae**
- Three cheek teeth each on maxilla and mandible; these teeth higher and lacking the fine ridges. 3
3. Cheek teeth prismatic and very tall. **Arvicolidae**
- Cheek teeth cuspidate and relatively low-crowned. 4
4. Cusps forming a few chevrons; upper cheek teeth with three longitudinal cusp rows. **Muridae**
- Cusps alternating in arrangement; upper cheek teeth with only two longitudinal cusp rows. **Cricetidae**

In the subsequent descriptions, Cricetidae is omitted, because it is represented by only one

specimen which was already described by KAWAMURA (1977b).

Family **Sciuridae** GRAY, 1821

Four sciurid genera such as *Sciurus*, *Tamias*, *Petaurista* and *Pteromys* are known from the present Japanese Islands. Their distribution within the islands shows a characteristic pattern. *Tamias* is found only in Hokkaido, while *Petaurista* is distributed in Honshu, Shikoku and Kyushu, but not in Hokkaido. Although *Sciurus* and *Pteromys* are found in both of the areas, each of them is specifically different in each area. The fossils of the sciurid genera except *Tamias* are recorded from the Quaternary sediments of Honshu, Shikoku and Kyushu. They suggest that such a distribution pattern has unchanged since the late Middle Pleistocene.

A key to the genera based on dental characters is given below.

Key to the genera of the Japanese sciurids

1. Size smaller; lophodont condition less advanced, so that tooth pattern is more or less cuspidate especially in lower cheek teeth; upper cheek teeth without posterior cross loph and posterolingual diagonal flexus; antero-lingual wall of protocone never depressed; hypocone distinguishable; metaloph somewhat cuspidate but continuous in P^4 , M^1 and M^2 ; this loph completely absent in M^3 ; lower cheek teeth with simple pattern; talonid basin flattened; metalophid sometimes present but very weak; hypolophid always absent; paraconid low and indistinct, and separated from protoconid; antero-buccal wall of crown never depressed in every lower cheek tooth. 2
- Size smaller; lophodont condition somewhat advanced in upper cheek teeth, but lower cheek teeth more or less cuspidate; upper cheek teeth with posterior cross loph and posterolingual diagonal flexus; antero-lingual wall of protocone remarkably depressed; hypocone distinguishable; metaloph always present in M^3 as in other upper cheek teeth; but this loph incomplete, because metaconule is isolated from endoloph and metacone by two deep longitudinal grooves (posterolingual diagonal flexus and lingual part of postfossette); lower cheek teeth with simple pattern; talonid basin flattened without remarkable lophs; metalophid usually present but weak; hypolophid present in M_3 , but absent or vestigial in other lower cheek teeth; paraconid better developed and connected with protoconid by a narrow ridge; buccal wall of this ridge depressed in M_2 and M_3 ***Pteromys***
- Size much larger; lophodont condition highly advanced in both upper and lower cheek teeth; upper cheek teeth with posterior cross loph and posterolingual diagonal flexus; antero-lingual wall of protocone sometimes depressed but sometimes smoothed out; hypocone almost indistinguishable; metaloph complete in every upper cheek tooth, and metaconule merged into this loph; lower cheek teeth extremely complicate with several transverse, diagonal and longitudinal lophs, so that talonid basin is divided into several grooves and pits; hypolophid always high and distinct; paraconid better developed and connected with protoconid to form anterior part of ectolophid; this part always grooved buccally. ***Petaurista***
2. Size larger; lower incisor without striations. ***Sciurus***
- Size smaller; lower incisor with striations (hitherto unknown as fossil state in Japan). ***Tamias***

Subfamily **Sciurinae** BAIRD, 1857

Genus ***Sciurus*** LINNAEUS, 1758

Remarks

Many living species are known from North and South America, but only three living species are generally recognized in Eurasia. These Eurasian species are represented by *S. anomalus* SCHREBER, *S. vulgaris* LINNAEUS and *S. lis* TEMMINCK. The first species is known from Southwest Asia, while the second is extensively distributed in the Palaearctic Region from

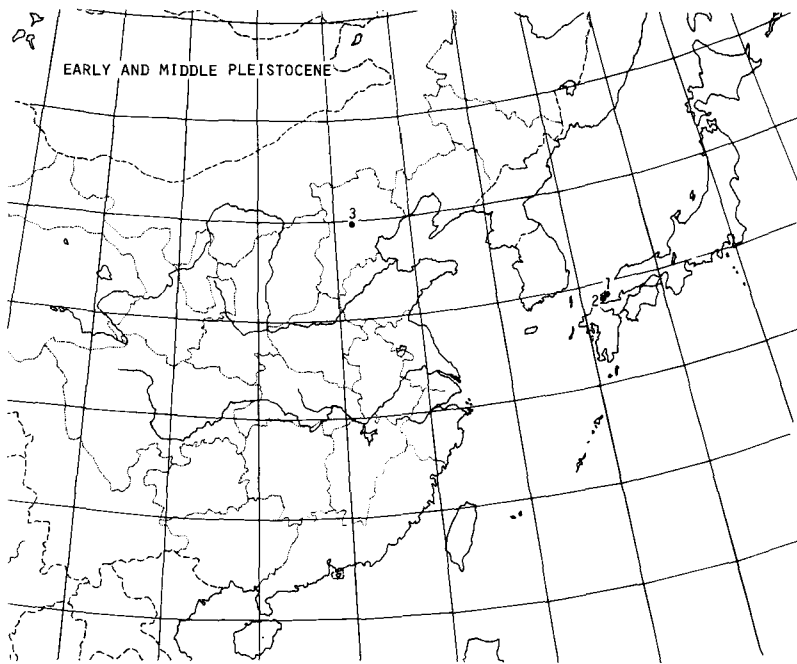


Fig. 79. Early and Middle Pleistocene fossil localities of *Sciurus* in East Asia. 1, Ikumo Quarry; 2, Locality 3 of Ube Kosan Quarry; 3, Localities 3, 9, 12, 15 and 20 of Choukoutien. For detailed explanation see Table 18.

Table 18. Early and Middle Pleistocene fossil localities of *Sciurus* in East Asia. The numbers on the left side correspond to those in Fig. 79.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
EARLY PLEISTOCENE			
3. Locality 12 of Choukoutien	<i>Sciurus</i> sp.	Teilhard (1938)	
MIDDLE PLEISTOCENE			
1. Ikumo Quarry	<i>Sciurus</i> sp.	Hasegawa (1963, 1966)	No descriptions are given.
2. Locality 3 of Ube Kosan Quarry	<i>Sciurus lis</i>	This paper	
3. Locality 3 of Choukoutien	? <i>Sciurus</i> sp.	Pei (1936)	
3. Locality 9 of Choukoutien	<i>Sciurus</i> sp.	Teilhard (1936)	
3. Locality 15 of Choukoutien	<i>Sciurus</i> sp.	Pei (1939)	No descriptions are given.
3. Locality 20 of Choukoutien	<i>Sciurus</i> sp.	Chia et al. (1959)	Ditto.

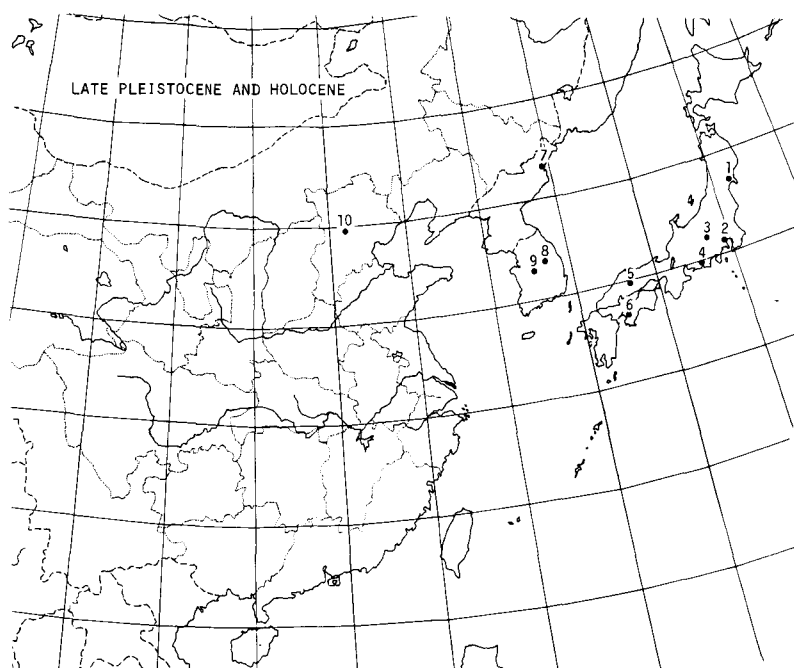


Fig. 80. Late Pleistocene and Holocene fossil localities of *Sciurus* in East Asia. 1, Aoshima Shellmound; 2, Miyanomae Shellmound; 3, Tochibara Rockshelter Site; 4, Shiraiwa Mine; 5, Kannondo Cave Site (Late Pleistocene horizons) and Anagami Rockshelter Site; 6, Shikimizu Quarry; 7, Nongpo-ri; 8, Chommal Yonggul Cave; 9, Turubong Cave; 10, Upper Cave of Choukoutien. For detailed explanation see Table 19.

Europe to Eastern Siberia, Northeastern China, Korea and Hokkaido. The third species is restricted to Honshu, Shikoku and Kyushu.

Although the revision of the Chinese fossils which were allocated to *Sciurus* by the previous authors is required*, these fossils are exclusively reported from several localities of Choukoutien with various geological ages (Fig. 79 and Table 18). All of them are referred to *Sciurus* sp. On the other hand, the fossils of *Sciurus* are more extensively recorded in Japan. However their occurrence is rather rare in each locality. These fossils are mostly identified as *S. lis* as shown in Tables 18 and 19.

***Sciurus lis* TEMMINCK, 1844**

(Figs. 81, 85)

Sciurus lis, TEMMINCK 1844, *Fauna Japonica*, Mamm., 45.

Synonym (living forms) —

Sciurus lis TEMMINCK; THOMAS 1905, *Proc. Zool. Soc. London*, **1905**, **2**, 347.

* "*Sciurus* cf. *dauricus*" from Locality 3 of Choukoutien described by PEI (1936), at least, should be transferred to *Sciurotamias*, if this form is comparable with *dauricus* as PEI stated.

Table 19. Late Pleistocene and Holocene fossil localities of *Sciurus* in East Asia. The numbers on the left side correspond to those in Fig. 80.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
LATE PLEISTOCENE			
4. Shiraiwa Mine	<i>Sciurus lis</i>	Hasegawa (1966); Kowalski & Hasegawa (1976)	Kowalski & Hasegawa identified this form as <i>Sciurus vulgaris</i> .
5. Kannondo Cave Site (Late Pleist. horizons)	<i>Sciurus lis</i>	Kawamura et al. (1986); this paper	
6. Shikimizu Quarry	<i>Sciurus lis</i> or ? <i>Sciurus</i> sp.	Shikama & Hasegawa (1962); Hasegawa (1966)	No descriptions are given.
8. Chommal Yonggul Cave	<i>Sciurus</i> sp.	Sohn (1984)	Ditto.
9. Turubong Cave	<i>Sciurus</i> sp.	Sohn (1984)	Ditto.
10. Upper Cave of Choukou-tien	? <i>Sciurus</i> sp.	Pei (1940)	
HOLOCENE			
1. Aoshima Shellmound	? <i>Sciurus lis</i>	Kato & Goto (1975)	No descriptions are given.
2. Miyanomae Shellmound	<i>Sciurus lis</i>	Naora (1944)	Ditto.
3. Tochibara Rockshelter Site	<i>Sciurus lis</i>	Miyao et al. (1980)	Ditto.
5. Anagami Rockshelter Site	<i>Sciurus lis</i>	Kawamura (1983)	Ditto.
7. Nongpo-ri	<i>Sciurus vulgaris</i>	Sohn (1984)	Ditto.

Sciurus lis TEMMINCK; KISHIDA 1924, *Honyudobutsu Zukai* (Monogr. Japanese Mamm.), 150–151.

Sciurus lis TEMMINCK & SCHLEGEL; KURODA 1940, *Monogr. Japanese Mamm.*, 80–81.

Sciurus vulgaris lis TEMMINCK; IMAIZUMI 1949, *Nat. Hist. Japanese Mamm.*, 216–217.

Sciurus vulgaris lis TEMMINCK; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian Mammals*, 473.

Sciurus vulgaris lis TEMMINCK & SCHLEGEL; KURODA 1953, *Nippon Jurui Zuzetsu* (Monogr. Japanese Mamm.), 74.

Sciurus lis TEMMINCK; IMAIZUMI 1960, *Coloured Illustr. Mamm. Japan*, 117–118.

Sciurus vulgaris lis TEMMINCK; SIDOROWICZ 1971, *Zool. Anz.*, **187**, 137.

Sciurus lis; CORBET 1978, *The Mammals of the Palaearctic Region*, 78.

Synonym (fossil forms) —

Sciurus vulgaris LINNAEUS; KOWALSKI and HASEGAWA 1976, *Bull. Nat. Sci. Mus.*, Ser. C, **2**, 33–34; from Shiraiwa Mine.

Sciurus lis; KAWAMURA 1983, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, **6**, 58; from Anagami Rockshelter Site.

Sciurus lis TEMMINCK; KAWAMURA et al. 1986, *Ibid.*, **9**, 71; from Kannondo Cave Site.

Materials —

Locality 3 of Ube Kosan Quarry

1 isolated M¹ from Layer 12 (KUJC98064); 1 isolated P₄ from Layer 17 (KUJC98065).

Kannondo Cave Site (specimen numbers are prefixed by HUA)

1 isolated M¹ (K00361) from Horizon P; 1 isolated dP₄ (K00359) and 1 isolated M₁ (K00360) from Horizon N.

Diagnosis

M¹ with four transverse lochs which are more or less cuspidate; bottoms of valleys among these lochs smoothed out; lingual wall of endoloph ungrooved; hypocone distinguishable; anteroloph and posteroloph lower than other two lochs; mesostyle present, but posterior cross loph and posterolingual diagonal flexus absent; metaloph continuous.

dP₄ and M₁ with simple pattern; cusps rather well-defined, and arranged on margin of crown; talonid basin wide and its floor smoothed; no transverse lochs (including hypolophid) present in this basin; antero-buccal wall of crown never depressed; paraconid separated from protoconid in M₁, but absent in dP₄.

Description

The crown is nearly as hypsodont as those of the Japanese species of *Petaurista* and *Pteromys* (Fig. 85). However the lophodont condition is not so advanced as those of the latter two genera. The cusps which form each loph are therefore recognizable not only in dP₄ and M₁ but also in M¹.

M¹ —

M¹ is represented by two specimens (KUJC98064 and HUA-K00361). The occlusal outline of the crown is subquadrate with round lingual margin in the former specimen, but more trapezoidal in the latter.

The crown comprises four transverse lochs which are connected with the lingual longitudinal loph (endoloph). Among these lochs, three transverse valleys are observed. The floors of these valleys are smoothed.

The protocone is the largest cusp, and forms the most part of the endoloph. This cusp is semicircular in occlusal view, and its lingual wall is smoothed and ungrooved. The hypocone is much smaller and lower than the protocone. It is attached on the posterior face of the protocone to constitute the remaining part of the endoloph.

The anteroloph branches from the endoloph at right angles. This loph is lower and slenderer than the protoloph. The parastyle is represented by the buccal swelling of the anteroloph. This cusp is considerably higher than the remaining part of the loph. The valley between the anteroloph and protoloph is slender, and opens buccally.

The protoloph runs nearly parallel to the anteroloph. This loph is divided into three cusps in KUJC98064. Among these cusps, the buccal cusp, paracone, is larger and much higher than other two cusps. The central cusps, protoconule, is somewhat elongated transversely. The lingual cusp is the smallest of them and slightly separated from the protoconule and endoloph by fine grooves on both sides. In HUA-K00361, however, the central and lingual cusps are not observable, while the paracone is remarkably enlarged.

The valley between the protoloph and metaloph are much wider than the other two valleys (twice or more). This valley opens buccally through a wide opening. The mesostyle is observed on the bottom of this opening. It is indistinct and much lower than the paracone.

The metaloph branches somewhat diagonally from the endoloph. In KUJC98064, this loph is also divided into four cusp such as metacone, metaconule and two additional cusplets.

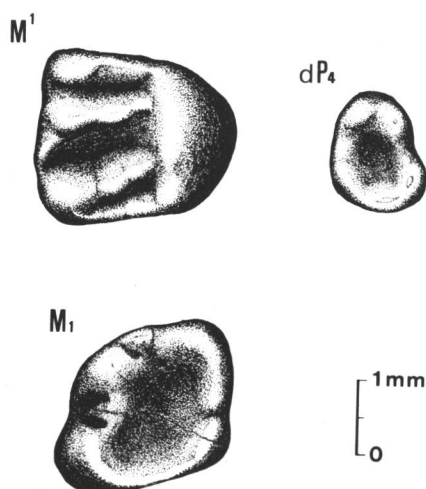


Fig. 81. *Sciurus lis*. Occlusal view of the cheek teeth. M¹, right M¹ from Layer 12 of Locality 3 of Ube Kosan Quarry (KUJC98064); dP₄, right dP₄ from Horizon N of Kannondo Cave Site (HUA-K00359); M₁, left M₁ from the same horizon of the same site (HUA-K00360).

The metacone is much larger and higher than the other cusps. The most lingual cusplet is quite indistinct. In HUA-K00361, however, the metaloph comprises only two cusps with nearly the same size.

The valley between the metaloph and posteroloph is slender and the narrowest of the three valleys. The buccal end of this valley is closed by the connection of the metacone with the posteroloph.

The posteroloph extends transversely along the posterior margin of the crown. It is lower than the metaloph, and is composed of three cusplets. The lingual cusplet is the largest of the three, but the others are small and indistinct.

M¹ has three roots. However they can be observed only in HUA-K00361, where the lingual and antero-buccal roots are preserved. The cross sections of these roots are round. The lingual root seems to be larger than the other two buccal roots.

dP₄ —

dP₄ is represented by only one specimen (HUA-K00359) which is slightly worn. Although the most part of the anterior root is lost, the crown and posterior root are well preserved.

The outline of the crown is ovate in occlusal view. Five low cusps are arranged on the margin of the crown, and surround a wide talonid basin. These cusps are assigned to protoconid, hypoconid, entoconid, mesostylid and metaconid. The floor of the talonid basin is smoothed out. This basin opens lingually between the metaconid and entoconid as well as buccally between the protoconid and hypoconid.

The metaconid is higher and more distinct than the protoconid. These cusps are continuous and coalescent to each other. The posterolophid connects the hypoconid with the entoconid to form the posterior wall of the crown. The mesoconid is attached on the anterior face of the hypoconid. It is vestigial and almost indistinguishable. The mesostylid is isolated

from the metaconid and entoconid, but much lower than these cusps.

dP₄ has two thick roots. These roots are elliptical in cross section. The anterior root extends antero-inferiorly, while the posterior one extends postero-inferiorly.

P₄ —

Only one specimen (KUJC98065) is available for the present study. Because the crown of this specimen is strongly worn, the pattern can not be observed. Nevertheless the roots are well preserved.

The observation of the specimen indicates that P₄ has two roots with elliptical cross sections. The posterior root is thicker than the anterior one. In cross section, the former is more elongated transversely than the latter.

M₁ —

M₁ is also represented by only one specimen (HUA-K00360) which is almost unworn.

The outline of the crown is trapezoidal with round corners in occlusal view. The basic pattern is equivalent to that of dP₄. The cusps are connected to each other to form low ridges on the margin of the crown. A wide talonid basin is enclosed by these ridges as in dP₄. The floor of the basin is smoothed.

The metaconid is the highest and largest cusp, which is situated at the antero-lingual corner of the crown. Because its postero-buccal face is flattened, this cusp is triangular in occlusal view. The mesostylid is ridge-like and fused with the metaconid. A remarkable notch is observed between the mesostylid and entoconid. The entoconid at the postero-lingual corner of the crown is elongated and shows more or less ridge-like feature. From this cusp, the posterolophid extends buccally along the posterior margin of the crown to reach the hypoconid. The hypoconid, the second largest cusp, is situated at the postero-buccal corner of the crown. Between this cusp and the protoconid, there is a broad buccal valley. This valley is short, but divided into two parts by the mesoconid. The protoconid at the antero-buccal corner is smaller than the hypoconid, but these two cusps have nearly the same height. This level is also near to the tops of the mesostylid and entoconid. The mesoconid is, however, much lower than the level. This cusp is much smaller than the protoconid, and divided into two parts by a fine transverse groove. The mesoconid connects with the protoconid and hypoconid by short ridges. The paraconid is as large as the mesoconid, but lower than the protoconid. It somewhat elongates transversely, and is separated from the protoconid and metaconid by fine grooves on both sides. The metalophid is almost indistinguishable.

The present molar is four-rooted. The postero-buccal root is the largest and has an elliptical cross section. The antero-lingual and postero-lingual roots have nearly the same size, but are somewhat smaller than the postero-buccal root. These two roots are round in cross section. The antero-buccal root with a round cross section is the smallest of the four.

Measurements

The length and width of the crown are measured as follows (in mm):

	M ¹		dP ₄	M ₁
	KUJC98064	HUA-K00361	HUA-K00359	HUA-K00360
Length	2.28	2.23	1.59	2.17
Width	2.62	2.52	1.26	2.45

Comparisons

Although several authors treated *lis* as a subspecies of *S. vulgaris*, the author agrees with the opinions of IMAIZUMI (1960), CORBET (1978), and HONACKI *et al.* (1982) regarding it as a full species. In comparison with the living *S. lis* collected from Honshu, no significant differences in tooth pattern and size are found in the present fossils. Because *S. vulgaris* is not available for the present study as comparative recent materials, its cheek teeth can not be closely compared with the present fossils. But judging from the illustrations of the cheek teeth of *S. vulgaris* provided by MILLER (1912), STEHLIN and SCHAUB (1951), SULIMSKI (1964) and WILTAFSKY (1978), their patterns are very similar to those of the present fossils. On the other hand, WILTAFSKY (1978) mapped the size variation of *S. vulgaris* throughout its vast range. His map clearly shows that *S. vulgaris* distributed in Hokkaido and the adjacent continent to Japan are considerably larger than *S. lis*. Such a size difference is also seen in the measurements of *S. vulgaris* in Hokkaido and *S. lis* given by IMAIZUMI (1960). In spite of the similarity in tooth pattern to *S. vulgaris*, the coincidence with *S. lis* in size as well as in tooth pattern suggests that the present fossils are most probably assigned to *S. lis*.

Almost all the previous authors who recorded the fossils of *Sciurus* from Japan gave only the specific names in their faunal lists. Therefore these records are useless in the comparisons with the present fossils. Brief description and measurements of *S. vulgaris* (assignable to *S. lis* in the present treatment) from Shiraiwa Mine were given by KOWALSKI and HASEGAWA (1976). Because it is represented by only two upper incisors, the comparison with the present fossils is also impossible.

The Chinese Pleistocene "*Sciurus*" comparable with the present fossils are also few. *Sciurus* sp. from Locality 12 of Choukoutien described by TEILHARD (1938) differs from the present fossils by smaller size, by the continuation of mesostylid with entoconid in M₁ and by poorly developed posterolophid and mesoconid in the same tooth. "?*Sciurus* sp." from Locality 3 of Choukoutien (PEI, 1936) is also different from them in the following points: 1. smaller size; 2. posterior part of metaconid poorly developed in M₁; 3. talonid basin open lingually between metaconid and mesostylid in the same tooth. "?*Sciurus* sp." from the Upper Cave of Choukoutien is considered to be the same form as that from Locality 3 (PEI, 1940). Although its description is quite insufficient, this form is clearly smaller than the present fossils.

Two extinct species of *Sciurus* are known from Europe. One is *S. whitei* HINTON of the Middle Pleistocene, and another is *S. warthae* SULIMSKI of the Pliocene and Early Pleistocene. *S. whitei* was first proposed by HINTON (1914) on the basis of a single P⁴. Subsequently JÁNOSSY (1962) introduced a new subspecies, *S. whitei hungaricus*, for several remains including M₁ from Hungary, and considered it as an intermediate form between *S. vulgaris* and *S. whitei*.

In comparison with this subspecies, the present fossils differ in having larger size and less independent mesostylid. On the basis of the original description and figure of *S. warthae* by SULIMSKI (1964), this species is also different from the present fossils in having larger size, well-isolated mesoconid and wide valley between metaconid and entoconid formed by the absence of mesostylid.

Discussion

In spite of the scarcity of the materials, there are no significant differences between the Pleistocene fossils described here and the recent *S. lis*. The other Quaternary fossils previously recorded from Honshu and Shikoku seem to be conspecific with *S. lis*. Therefore *S. lis* can be considered to inhabit these areas since the middle Middle Pleistocene. As generally understood, *S. lis* is closely related to *S. vulgaris*, and was possibly originated from the latter species. The ancestor of *S. lis* seems to have immigrated from the boreal continent in the periods earlier than the middle Middle Pleistocene, and settled in Japan south of the Tsugaru Strait. The speciation of this species may be attributable to the isolation of this area from Hokkaido and the continent as islands.

S. lis is considered to be a squirrel adapted to temperate forests from the recent habitats of the species. The occurrence of this species, therefore, indicates sylvan environments. On the other hand, the sciurines which inhabit grasslands or rocky areas such as *Spermophilus*, *Marmota* and *Sciurotamias* are unknown from the Quaternary sediments of Japan. In addition to this fact, the occurrences of *S. lis* from various fossil localities in Japan roughly suggest that the temperate sylvan environments like the present vegetation have been predominant since the middle Middle Pleistocene in the main part of Japan.

Subfamily **Petauristinae** SIMPSON, 1945

Genus **Petaurista** LINK, 1795

The Japanese petauristines are easily divided into two groups by the remarkable differences in size and tooth pattern. On the basis of the key to the living genera provided by MCKENNA (1962) and the descriptions of the fossil genera by MEIN (1970), the large-sized group with the following dental characters can be allocated to the genus *Petaurista*, while the small-sized group is referable to the genus *Pteromys* which is described in the next section.

Characters

The size is medium to large as petauristines. The upper incisor is ungrooved. The cheek teeth are highly lophodont. The bottoms of the valleys on their crowns are smoothed.

P³ is conical and unicuspid. The size and pattern of P⁴ approach to those of the upper molars, but its occlusal outline is somewhat more triangular or trapezoidal than those of the molars which are transversely elliptical. P⁴ and the molars have three main transverse ridges. Among these, two deep valleys are formed, which open buccally. In these teeth, the protocone and hypocone are almost merged to form a high longitudinal wall on the lingual side. The

mesostyle and mesoloph are absent except in P^4 where a small mesostyle is observed. The metaconule is well merged into the metaloph and indistinguishable from this ridge. The posterior cross loph runs from the metaconule at right angles with the metaloph. It separates the posterolingual diagonal flexus from the postfossette. The posteroloph is observable in the upper molars.

The lower cheek teeth have very complicate patterns with many ridges. The mesoconid is well developed. Two or three short diagonal ridges are present in the metaconid-metastylid chaos. They are sometimes crenulated, or sometimes connect with other ridges, or are sometimes interrupted. The hypolophid and posterolophid are well developed, and usually connect the entoconid with the mesoconid and with the hypoconid respectively. P_4 is molariform.

Key to the species of the Japanese *Petaurista*

1. Size much larger; pattern of M^2 more complicate; postfossette larger than or equal to posterolingual diagonal flexus in the same molar. *Petaurista leucogenys*
2. Size much smaller; pattern of M^2 simpler; postfossette much smaller than posterolingual diagonal flexus in the same molar. *Petaurista* sp.

Geological and geographical distribution of *Petaurista*

The living species of *Petaurista* are known mainly from the Oriental Region. Their distribution covers Japan (except Hokkaido), Taiwan, Central and South China, Indochina, Indonesia, Nepal, Tibet and India. Their occurrences from Korea and northeastern part of China are doubtful as pointed out by JONES and JOHNSON (1965). Therefore Honshu is the northern limit of the recent distribution. The species of *Petaurista* generally inhabit dense forests.

The fossils of *Petaurista* are rare in all the fossil localities except the Holocene ones in Japan. It may be related to the arboreal habit of the genus.

The Middle Pleistocene fossils of *Petaurista* are reported from five localities in China and two localities in Japan (Fig. 82, Table 20). These localities are scattered over wide areas from south to north. It possibly indicates that the distribution of *Petaurista* were expanded more northwardly than in the present day in the continent. Taking the habitats of the living *Petaurista* into consideration, this northward expansion may be associated with the northward shifting of forests in the warmer periods of the Middle Pleistocene. The Middle Pleistocene fossils in China are assigned to *P. brachyodus* and *P. sp.*, while those in Japan are referred to *P. leucogenys*. Although these Chinese forms can not be sufficiently compared with *P. leucogenys*, they seem to be distinct from the latter species. If the Japanese species, *P. leucogenys*, were derived from a common ancestor to the Chinese forms, the time of speciation of *P. leucogenys* seems to be earlier than the middle Middle Pleistocene.

The Late Pleistocene records of *Petaurista* are very rare in China, but rather rich in Japan (Fig. 83, Table 21). The only record from China is *P. elegans* from Sanjiacun, Yunnan. Although *Aeretes*, an allied genus, is described from the Upper Cave of Choukoutien (originally assigned to *Pteromys sulcatus* by PEI, 1940), *Petaurista* is unknown from Central and North China.

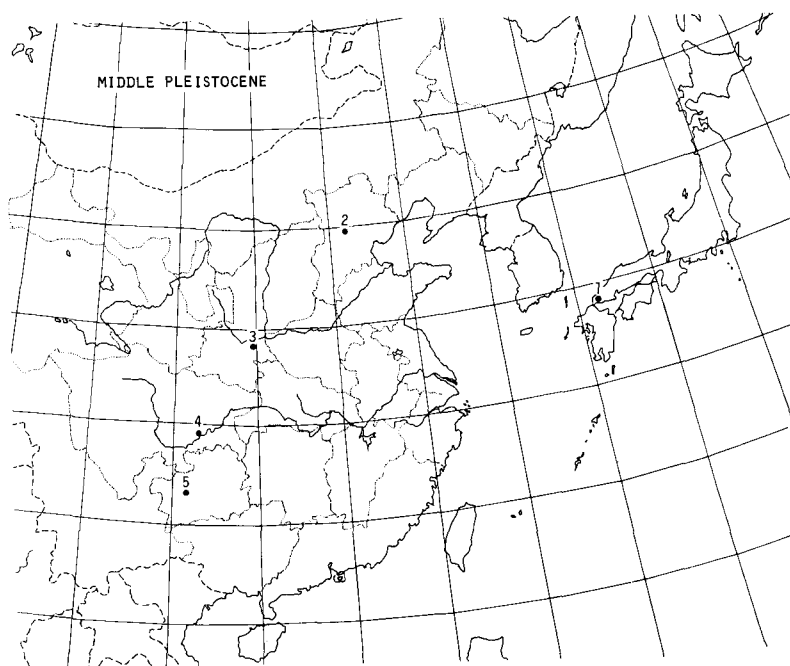


Fig. 82. Middle Pleistocene fossil localities of *Petaurista* in East Asia. 1, Akiyoshi Area (Ando Quarry and Locality 3 of Ube Kosan Quarry); 2, Locality 1 of Choukoutien; 3, Gongwangling at Lantian; 4, Koloshan; 5, Chihchin. For detailed explanation see Table 20.

Table 20. Middle Pleistocene fossil localities of *Petaurista* in East Asia. The numbers on the left side correspond to those in Fig. 82.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS	
JAPAN				
1. Ando Quarry	<i>Petaurista leucogenys</i>	Hasegawa (1966, 1972); Kowalski & Hasegawa (1976)	Young originally assigned to <i>Pteromys brachyodus</i> .	
1. Locality 3 of Ube Kosan Quarry	<i>Petaurista leucogenys</i>	This paper		
CHINA				
2. Locality 1 of Chou-koutien	<i>Petaurista brachyodus</i>	Young (1934); Kahlke & Chow (1961)		
3. Gongwangling at Lantian	<i>Petaurista</i> sp.	Hu & Qi (1978)		
4. Koloshan	<i>Petaurista</i> cf. <i>brachyodus</i> <i>Petaurista</i> sp.	Young & Liu (1950)		
5. Chihchin	<i>Petaurista</i> cf. <i>brachyodus</i>	Hsu et al.(1957)		

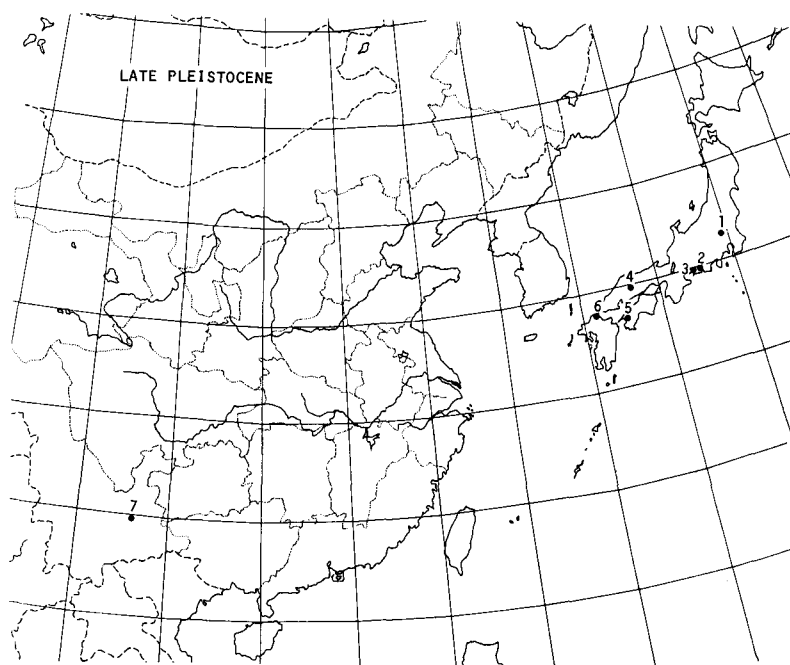


Fig. 83. Late Pleistocene fossil localities of *Petaurista* in East Asia. 1, Kuzuu Area (Miyata First Cave and Shimizu Sekkai Quarry at Yamasuge); 2, Shiraiwa Mine; 3, Suse Quarry (East Fissure); 4, Kannondo Cave Site (Late Pleistocene horizons); 5, Shikimizu Quarry; 6, Mejiro-do Cave; 7, Sanjiacun. For detailed explanation see Table 21.

On the other hand, the Japanese fossils are mostly identified as *P. leucogenys* as in the Middle Pleistocene localities.

Petaurista can not be found in any available reference which describes the Holocene mammalian remains of China. However it is abundantly reported from the Holocene sediments of Japan (mostly from the Neolithic archaeological sites; Fig. 84, Table 22). Almost all the fossils of *Petaurista* are allocated to *P. leucogenys*. *P. sp.* from the Holocene sediments of Tanuki-ana Cave is clearly different from *P. leucogenys*, but the affinity and origin of this form are not sufficiently understood owing to the extreme scarcity of specimen.

***Petaurista leucogenys* (TEMMINCK, 1827)**

(Figs. 85–90)

Pteromys leucogenys, TEMMINCK 1827, *Monogr. Mamm.*, 1, 27.

Synonym (living forms) —

Pteromys leucogenys; TEMMINCK 1844, *Fauna Japonica, Mamm.*, 46–47.

Petaurista leucogenys TEMMINCK; THOMAS 1905, *Proc. Zool. Soc. London*, 1905, 2, 344.

Petaurista leucogenys nikkonis THOMAS, *P. l. oreas* THOMAS and *P. l. leucogenys* (TEMMINCK); KISHIDA 1924,

Honyudobutsu Zukai (Monogr. Japanese Mamm.), 157–161. (excluding *P. l. hintonii*)

Petaurista leucogenys osui KURODA, *P. l. nikkonis* THOMAS, *P. l. oreas* THOMAS, *P. l. tosae* THOMAS and *P. l.*

Table 21. Late Pleistocene fossil localities of *Petaurista* in East Asia. The numbers on the left side correspond to those in Fig. 83.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
JAPAN			
1. Miyata First Cave	<i>Petaurista</i> cf. <i>leucogenys</i>	Shikama (1949)	No descriptions are given.
1. Shimizu Sekkai Quarry at Yamasuge	<i>Petaurista</i> sp.	Naora (1954)	
2. Shiraiwa Mine	<i>Petaurista leucogenys</i>	Kowalski & Hasegawa (1976)	
3. Suse Quarry (East Fissure)	<i>Petaurista leucogenys</i>	This paper	
4. Kannondo Cave Site (Horizons M to P)	<i>Petaurista leucogenys</i>	Kawamura (1980, 1981, 1982); Kawamura et al. (1986); this paper	This record without descriptions is doubtful, because <i>Petaurista</i> from this locality is not listed in Shikama & Hasegawa (1962) and Kowalski & Hasegawa (1976).
5. Shikimizu Quarry	<i>Petaurista leucogenys</i>	Hasegawa (1966)	
6. Mejiro-do Cave	<i>Petaurista leucogenys</i>	Sotsuka (1972a, b); Kawamura & Sotsuka (1984)	No descriptions are given.
CHINA			
7. Sanjiacun	<i>Petaurista elegans</i>	Qiu et al. (1984)	

leucogenys (TEMMINCK); KURODA 1940, *Monogr. Japanese Mamm.*, 88–90. (excluding *P. l. hintoni*)
Petaurista leucogenys (TEMMINCK); IMAIZUMI 1949, *Nat. Hist. Japanese Mamm.*, 227–230.
Petaurista leucogenys TEMMINCK; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian Mammals*, 464–465 (in part; excluding *P. l. xanthotis* and *P. l. hintoni*).
Petaurista leucogenys TEMMINCK; KURODA 1953, *Nippon Jurui Zusetsu (Monogr. Japanese Mamm.)*, 77.
Petaurista leucogenys TEMMINCK; IMAIZUMI 1960, *Coloured Illustr. Mamm. Japan*, 122–125 (in part).
Petaurista leucogenys; CORBET 1978, *The Mammals of the Palaearctic Region*, 86 (in part).

Synonym (fossil forms) —

Petaurista cfr. *leucogenys* (TEMMINCK); SHIKAMA 1949, *Sci. Rep. Tohoku Univ.* 2nd Ser. (Geol.), **23**, 114–115; from Miyata First Cave.
Petaurista leucogenys (TEMMINCK); KOWALSKI and HASEGAWA 1976, *Bull. Nat. Sci. Mus.*, Ser. C, **2**, 34–36; from Ando Quarry and Shiraiwa Mine.
Petaurista leucogenys (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.
Petaurista leucogenys (TEMMINCK); KAWAMURA and TAMIYA 1980, *Bull. Akiyoshi-dai Mus. Nat. Hist.*, (15), 32; from Tanuki-ana Cave.
Petaurista leucogenys (TEMMINCK); KAWAMURA 1980, 1981, 1982, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, **3**, 65; **4**, 69; **5**, 60; from the Late Pleistocene horizons of Kannondo Cave Site.
Petaurista leucogenys; KAWAMURA 1983, *Ibid.*, **6**, 58; from Anagami Rockshelter Site.
Petaurista leucogenys; KAWAMURA and SOTSUKA 1984, *Bull. Kitakyushu Mus. Nat. Hist.*, (5), 172; from Mejiro-do Cave, Ninjinkubo First Cave and Ojika-do Cave.
Petaurista leucogenys (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.

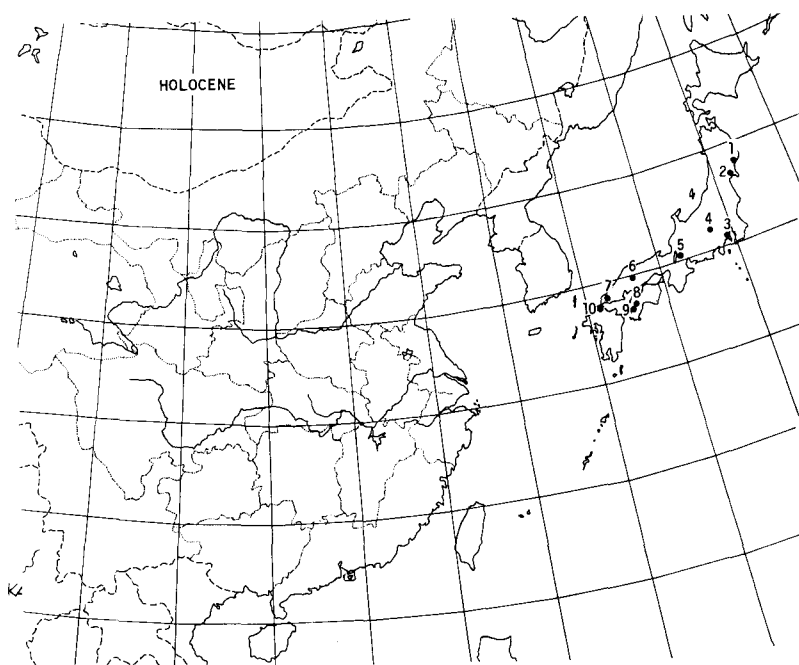


Fig. 84. Holocene fossil localities of *Petaurista* in East Asia. 1, Jaodo Cave; 2, Aoshima Shellmound; 3, Sugita Shellmound; 4, Tochibara Rockshelter Site; 5, Same Cave; 6, Taishaku Area (Kannondo Cave Site, Anagami Rockshelter Site and Domen Cave Site); 7, Akiyoshi Area (Tanuki-ana Cave and Makurazino-ana Cave); 8, Kamikuroiwa Rockshelter Site; 9, Kurosegawa Cave; 10, Hirao-dai Area (Ninjinkubo First Cave, Ojika-do Cave, Oiwa-ana Cave and Hato-ana Cave). For detailed explanation see Table 22.

Materials —

MIDDLE PLEISTOCENE LOCALITY

Locality 3 of Ube Kosan Quarry

1 isolated M_3 from Layer 6 (KUJC98061); 1 isolated M^1 from Layer 8 (KUJC98062); 1 isolated M^3 from Layer 9 (KUJC98063).

LATE PLEISTOCENE LOCALITIES

Kannondo Cave Site (specimen numbers are prefixed by HUA)

Horizon P: 1 fragmental M_2 (K00569); 1 isolated M_3 (K00570).

Horizon O (lower part): 1 mandible fragment without teeth (K00571); 1 isolated M_3 (K00572).

Horizon O (upper part): 4 isolated upper I (K00573–00576); 1 isolated M^1 (K00577); 3 isolated lower I (K00578–00580); 1 isolated M_1 (K00581); 1 isolated M_2 (K00582); 1 isolated M_3 (K00583).

Horizon N: 1 mandible with I (K04148); 1 isolated lower I (K00584); 1 lower incisor fragment (K00585); 1 isolated M_3 (K00586).

Horizon M (lower part): 1 isolated M^2 (K00587); 1 isolated M_2 (K00588); 1 isolated M_3 (K00589).

Horizon M (upper part): 4 isolated upper I (K00590–00593); 1 isolated M^3 (K00594); 1 isolated lower I (K00595); 1 isolated dP_4 (K00596); 1 incisor fragment (K00597).

Suse Quarry (East Fissure)

1 mandible with I, M_1 , M_2 and M_3 (MATSUHASHI Collection; unnumbered).

Table 22. Holocene fossil localities of *Petaurista* in East Asia. The numbers on the left side correspond to those in Fig. 84.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
JAPAN			
1. Jaodo Cave	<i>Petaurista leucogenys nikkonis</i>	Kaneko (1967)	No descriptions are given.
2. Aoshima Shellmound	<i>Petaurista leucogenys</i>	Kato & Goto (1975)	Ditto.
3. Sugita Shellmound	<i>Petaurista leucogenys nikkonis</i>	Naora (1944)	Ditto.
4. Tochibara Rock-shelter Site	<i>Petaurista leucogenys</i>	Miyao et al. (1980)	Ditto.
5. Same Cave	<i>Petaurista leucogenys oreas</i>	Naora (1944); Shikama et al. (1952)	Ditto.
6. Kannondo Cave Site (Holocene horizons)	<i>Petaurista leucogenys</i>	Kawamura (1978, 1979 a); this paper	
6. Anagami Rockshelter Site	<i>Petaurista leucogenys</i>	Kawamura (1983); this paper	
6. Domen Cave Site	<i>Petaurista leucogenys</i>	This paper	
7. Tanuki-ana Cave	<i>Petaurista leucogenys</i> <i>Petaurista</i> Sp.	Kawamura & Tamiya (1980); this paper	
7. Makirazino-ana Cave	<i>Petaurista leucogenys</i>	Shikama & Okafuji (1958)	No descriptions are given.
8. Kamikuroiwa Rock-shelter Site	<i>Petaurista leucogenys nikkonis</i>	Kaneko (1967)	Ditto.
9. Kurosegawa Cave	<i>Petaurista leucogenys</i>	Akazawa et al. (1976)	Ditto.
10. Ninjinkubo First Cave	<i>Petaurista leucogenys</i>	Kawamura & Sotsuka (1984); this paper	
10. Ojika-do Cave	<i>Petaurista leucogenys</i>	Hasegawa et al. (1968); Kawamura & Sotsuka (1984); this paper	
10. Oiwa-ana Cave	<i>Petaurista leucogenys</i>	Sotsuka (1972a, b)	No descriptions are given.
10. Hato-ana Cave	<i>Petaurista leucogenys</i>	Hasegawa et al. (1968)	Ditto

HOLOCENE LOCALITIES

Kannondo Cave Site (specimen numbers are prefixed by HUA)

Horizon L: 1 isolated upper I (K00598).

Horizon K: 1 isolated upper I (K00599).

Horizon I: 1 mandible with P₄, M₁, M₂ and M₃ (K00600); 1 mandible with I, P₄, M₁ and M₂ (K00601); 1 mandible with I, M₁, M₂ and M₃ (K00602); 1 mandible without teeth (K00603); 1 isolated lower I (K00604); 1 isolated M₂ (K00605).Horizon H: 1 skull fragment (K00606); 1 maxilla with P³, P⁴, M¹, M² and M³ (K00607); 1 isolated upper I (K00608); 1 mandible with M₁ (K00609); 3 isolated lower I (K00610-00612).Horizon G: 1 skull fragment (K00613); 1 maxilla with I (K00614); 3 isolated upper I (K00615-00617); 1 mandible with I, P₄, M₁, M₂ and M₃ (K00618); 1 mandible with I, P₄, M₁ and M₂ (K00619); 1 mandible with I, M₁, M₂ and M₃ (K00620); 1 mandible without teeth (K00622); 1 isolated lower I (K00623); 1 isolated M₃ (K00624).Horizon F: 1 skull fragment (K00625); 1 maxilla with I (K00626); 1 isolated upper I (K00627); 1 mandible with I and P₄ (K00628); 1 mandible with M₁ (K00629); 1 isolated P₄ (K00630).Horizon E: 1 mandible with P₄, M₁, M₂ and M₃ (K00631); 1 isolated lower I (K00632).

- Horizon D: 1 maxilla with M¹ (K00633); 1 mandible with I, M₁ and M₂ (K00634).
- Horizon C: 1 maxilla with dP⁴, P³, P⁴, M¹ and M² (K00635); 1 maxilla with P⁴, M¹ and M² (K00636); 1 maxilla with M¹, M² and M³ (K00637); 1 maxilla without teeth (K00638); 2 isolated upper I (K00639, 00640); 1 isolated M³ (K00641); 1 mandible with I, P₄, M₁, M₂ and M₃ (K00642); 1 mandible with I, P₄, M₁ and M₂ (K00643); 1 mandible with I, dP₄, P₄ and M₁ (K00644); 1 mandible with I, M₁ and M₂ (K00645); 2 mandibles with P₄, M₁ and M₂ (K00646, 00647); 1 mandible with I (K00621); 2 mandibles without teeth (K00648, 00649); 8 isolated lower I (K00650–00657); 2 isolated M₂ (K00658, 00659); 3 isolated M₃ (K00660–00662).
- Horizon B: 1 mandible with I, P₄, M₁, M₂ and M₃ (K00663); 1 mandible with I, P₄, M₁ and M₂ (K00664).
- Horizon A: 1 mandible with I, P₄, M₁, M₂ and M₃ (K00665).
- Horizon unknown: 1 skull fragment (K00666); 1 maxilla with P⁴, M¹, M² and M³ (K00667); 1 maxilla with dP⁴ and P⁴ (K00668); 2 maxillae without teeth (K00669, 00670); 2 isolated upper I (K00671, 00672); 5 mandibles with I, P₄, M₁, M₂ and M₃ (K00673–00677); 1 mandible with P₄, M₁ and M₂ (K00678); 1 mandible with I and M₁ (K00679); 2 mandibles with P₄ and M₁ (K00680, 00681); 3 mandibles with I (K00682–00684); 1 isolated lower I (K00685); 1 isolated M₁ (K00686); 2 isolated M₂ (K00687, 00688).
- Domen Cave Site (Horizon unknown)
1 isolated P⁴ (HUA-D00001).
- Tanuki-ana Cave
Layer 4: 1 fragmental mandible without teeth (ASM 700014); 1 isolated lower I (ASM 700015); 1 isolated P₄ (ASM 700016); 2 isolated M₂ (ASM 700017, 700018).
Layers 3 to 2: 1 isolated M¹ (ASM 700020); 1 isolated M² (ASM 700021).
Layer 2: 1 skull fragment (ASM 700022); 1 isolated upper I (ASM 700023); 2 isolated dP⁴ (ASM 700024, 700025); 3 isolated M¹ (ASM 700026–700028); 1 isolated M² (ASM 700029); 2 isolated M³ (ASM 700030, 700031); 1 isolated P₄ (ASM 700032); 1 isolated M₁ (ASM 700033); 2 isolated M₂ (ASM 700019, 700034); 1 isolated M₃ (ASM 700035).
- Anagami Rockshelter Site (Grids A-0, A-1, B-0 and B-1; specimen numbers are prefixed by HUA)
1 isolated M³ from Layer 6 (A00001); 1 skull fragment (A00002) and 1 maxillary fragment (A00003) from Layer 4; 1 isolated M¹ from Layer 3 (A00004); 1 isolated upper I (A00005), 1 isolated lower I (A00006) and 1 isolated M₁ (A00007) from Layer 1.
- Ninjinkubo First Cave (SORSUKA Collection; all specimens are unnumbered)
2 premaxillae with upper I; 1 mandible with I, M₁, M₂ and M₃; 1 mandible with I and M₁; 1 mandible with I; 2 isolated lower I.
- Ojika-do Cave (SORSUKA Collection; all specimens are unnumbered)
1 isolated upper I and 1 mandible with M₁ and M₂ from Chamber 1; 1 isolated M₁ from Branch 1.

Diagnosis

Size the largest of the Japanese sciurids, and much larger than that of *Petaurista* sp. Cheek teeth not hypsodont, but nearly as high as those of *Sciurus lis* and *Pteromys momonga* (Fig. 85); P⁴ slightly larger than M¹; a shallow vertical groove usually present on the lingual face of protocone in upper cheek teeth except P³; transverse ridges of these teeth slightly crenulated; anterior cross loph poorly developed and never reaching anteroloph in any tooth; posterolingual diagonal flexus smaller than postfossette in upper molars; patterns of lower cheek teeth highly variable especially in metaconid-metastylid chaos and around entoconid.

Description

Maxilla and palatine (Fig. 86) —

The zygomatic plate is steeply tilted postero-inferiorly. The lower border of the infraor-

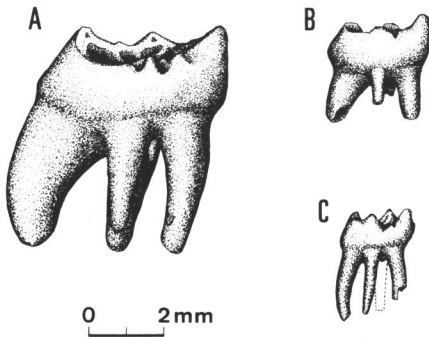


Fig. 85. Lingual view of the molars of the Japanese sciurids. In order to compare the hypsodonty, slightly worn specimens are illustrated. A, left M_2 of *Petaurista leucogenys* from Horizon I of Kannondo Cave Site (HUA-K00605); B, left M_1 of *Sciurus lis* from Horizon N of the same site (HUA-K00360); C, left M_1 of *Pteromys momonga* from the lower part of Horizon O of the same site (HUA-K00357).

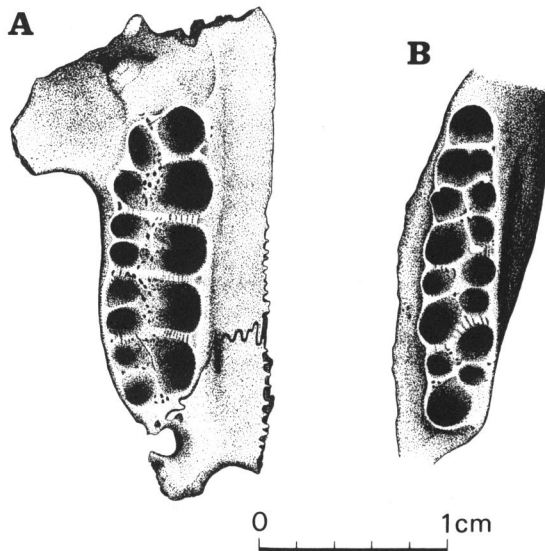


Fig. 86. *Petaurista leucogenys*. Alveolar patterns on maxilla (A) and mandible (B). A, right maxilla from Horizon C of Kannondo Cave Site (HUA-K00638); B, left mandible from the same horizon and site (HUA-K00648).

bital foramen is thickened to form a remarkable masseteric tubercle on the lowest part of this plate. The number of alveolar pits is totally 13 (one pit for P^3 , and three pits each for other cheek teeth). The pits of the lingual row are much larger than those of the buccal row. The foramen for the palatine vein opens immediately posterior to M^3 . This foramen is enlarged, and round in palatal view. On the other hand, the foramen for the palatine artery and palatine nerve is much smaller, and opens near the palato-maxillary suture immediately lingual to the lingual root of M^3 .

Upper incisor —

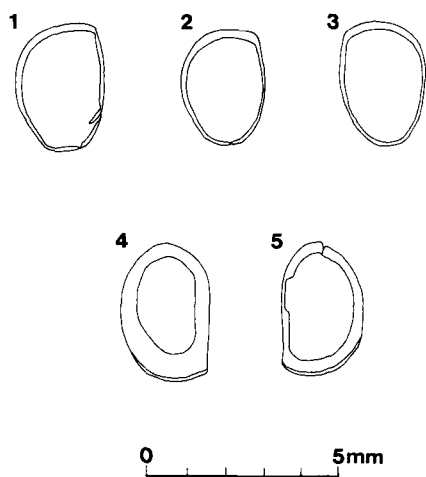


Fig. 87. Cross section of the incisors of *Petaurista leucogenys* observed at their posterior ends. All of the figured specimens were collected from the Holocene horizons of Kannondo Cave Site. 1, left upper incisor from Horizon L (HUA-K00598); 2, left upper incisor from Horizon C (HUA-K00639); 3, right upper incisor (exact horizon unknown; HUA-K00671); 4, left lower incisor from Horizon C (HUA-K00650); 5, right lower incisor from the same horizon (HUA-K00651).

The upper incisor is ungrooved and normal in shape as rodent incisors. The upper surface has deep orange colouration. The cross section is elliptical (Fig. 87).

dP⁴ —

The occlusal outline is near to a triangle with round corners. The occlusal pattern is simpler than that of *P⁴*, and characterized by three remarkable transverse ridges. The parastyle is elongated transversely to form the anterior ridge which is well separated from the middle ridge by the paraflexus. The protocene and hypocone seem to be merged to form a single large cusp on the postero-lingual part of the crown. The middle ridge (protoloph) runs transversely from this cusp to the paracone. A short spur is usually observed on the postero-lingual face of the paracone. The mesostyle is absent in the specimen from Horizon C of Kannondo Cave Site (HUA-K00635), but is represented by a short and slender ridge at the buccal entrance of the posterobuccal flexus in the two specimens from Layer 2 of Tanuki-ana Cave (ASM 700024, 700025). The merged protocone and hypocone, metaconule and metacone are connected to form the posterior ridge (metaloph). The metaconule is well developed, and is nearly equal to the paracone in size. It has one or two short posterior spurs in the specimens from Tanuki-ana Cave, but not in the specimens from Kannondo Cave Site. The metacone is weak, and smaller than the metaconule. The posterolingual diagonal flexus and postfossette are relatively short, and are connected posteriorly with each other by a very shallow transverse valley. The posteroloph is indistinct, and much lower than the metaloph.

dP⁴ has three roots.

P³ —

P³ is represented by only two specimens. Because *P³* of the specimen from Horizon C of Kannondo Cave Site (HUA-K00635) is unerupted, the following observation is based on another specimen from Horizon H of the same site (HUA-K00607) whose *P³* is unworn.

The crown is conical and unicuspid. The apex of the cusp is barely divided into two parts by two small depressions on both lingual and buccal sides. This tooth has only one root.

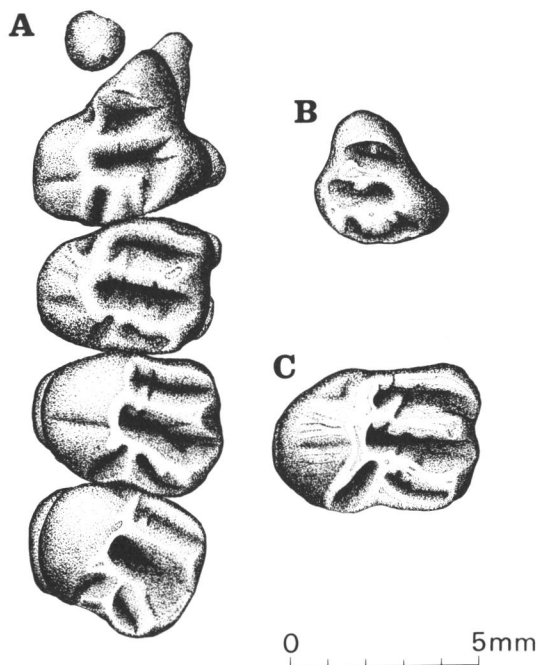


Fig. 88. *Petaurista leucogenys*. Occlusal view of the upper cheek teeth. A, left P³, P⁴, M¹, M² and M³ from Horizon H of Kannondo Cave Site (HUA-K00607); B, right dP⁴ from Horizon C of the same site (HUA-K00635); C, left M¹ from Layer 8 of Locality 3 of Ube Kosan Quarry (KUJC 98062).

P⁴ —

The occlusal outline is a rounded trapezoid. The parastyle is triangular in occlusal view, and is connected with the protocone by a low ridge. A remarkable depression is observed on the lingual wall of this ridge. The protoloph branches off from the anterior part of the protocone and extends buccally to the paracone. The protoconule is barely recognizable on the lingual part of this loph, but never forms the anterior cross loph. The protocone and hypocone is almost merged, but can be distinguished from each other by a faint groove on their lingual wall. The metaloph extends buccally from the hypocone to the metaconule. It sometimes reaches the metacone, but is sometimes separated from the latter cusp by a longitudinal groove. The posterior cross loph projects posteriorly from the metaconule to reach the posterior margin of the crown. The posteroloph is not observed. The posterolingual diagonal flexus is remarkably deep, and opens posteriorly. The postfossette is much smaller and shallower than this flexus. The mesostyle is present at the buccal entrance of the posterobuccal flexus. It is triangular in occlusal view.

P⁴ is three rooted.

M¹ —

The occlusal outline is transversely elliptical. The parastyle is slender and situated at the

antero-buccal corner of the crown. This cusp is well merged with the anteroloph, so that they are almost indistinguishable from each other. The lingual end of the anteroloph meets at right angles with the anterior ridge of the protocone (the anterior part of the endoloph) whose lingual wall is depressed. However this depression is not so remarkable as that of P^4 . The protoloph is set parallel to the anteroloph. The paracone and protoconule are well merged into the protoloph. The remnant of the anterior cross loph projects anteriorly from the protoconule, but it is so weak and short that it never reaches the anteroloph. The paraflexus is as broad as the posterobuccal flexus. The protocone and hypocone are merged to form the main part of the endoloph which is the highest part of the crown. These cusps are closely set, but are barely distinguishable from each other by a shallow groove on their lingual wall as in P^4 . The metaloph runs buccally from the hypocone to the metacone. The metaconule is represented by a small swelling on the lingual part of the metaloph, where the posterior cross loph branches out posteriorly. Another swelling is observed on the metaloph between the metaconule and metacone. Neither mesostyle nor mesoloph are present. The posterolingual diagonal flexus opens postero-lingually, while the postfossette is a closed groove and extends transversely along the metaloph. The posterior cross loph meets at right angles with the posteroloph which forms the posterior wall of the crown. The posteroloph is rather indistinct and much lower than the metaloph.

M^1 has three roots. The lingual root is much thicker than the antero-buccal and postero-buccal roots. The latter two have nearly the same size.

M^2 and M^3 —

The occlusal outlines and patterns of these teeth are basically identical with those of M^1 , but several minor differences are also observed as follows:

1. The occlusal outline of M^2 is almost identical with that of M^1 , but that of M^3 is more squarish.
2. The depression on the lingual wall of the anterior part of the endoloph is faint in M^2 , and absent from M^3 .
3. The groove on the lingual wall of the protocone is weaker in M^2 than in M^1 . Moreover it is absent from M^3 .
4. In M^2 , the metaloph is somewhat bent in the middle, and its buccal part extends postero-buccally (it is rather straight in M^1). The bend of the metaloph is more remarkable in M^3 than in M^2 .
5. The posterobuccal flexus is somewhat broader than the paraflexus in M^2 , while the former is as broad as the latter in M^1 . The former is much broader and deeper than the latter in M^3 .
6. The posteroloph is higher and more distinct in M^2 than in M^1 . It is much higher in M^3 where it attains approximately to the same height as the metaloph.

M^2 and M^3 have three roots each as M^1 . The shapes of these roots resemble those of M^1 .

Mandible (Fig. 86, 89) —

The mental foramen opens in the middle of the diastema on the buccal face of the horizontal ramus. The upper masseteric crest is inconspicuous and short. It extends postero-superiorly to form the anterior rim of the ascending ramus. The lower masseteric crest is also weak. It begins below the boundary between P_4 and M_1 , and extends postero-inferiorly. The symphyseal eminence is absent. The surface of the symphysis is remarkably rugose. The mandibular foramen opens immediately posterior to M_3 , and is situated at the level of the alveolar line. The mandibular incision is shallow. The top of the condylar process is only

slightly higher than the bottom of the mandibular incision, but much lower than the top of the coronoid process. The condyle is round in upper view. The angular process is remarkably broad, and its lingual face is broadly concave.

The number of alveolar pits is totally 14 (the anterior two pits for P_4 ; four pits each for other three teeth).

Lower incisor —

The shape is normal without any groove. The enamel-covered surface (lower face) is strongly pigmented in orange. The cross section is elliptical, and resembles that of the upper incisor (Fig. 87).

dP_4 —

dP_4 can be observed only in two specimens such as a left mandible with I, dP_4 , P_4 and M_1 from Horizon C of Kannondo Cave Site (HUA-K00644) and isolated dP_4 from the upper part

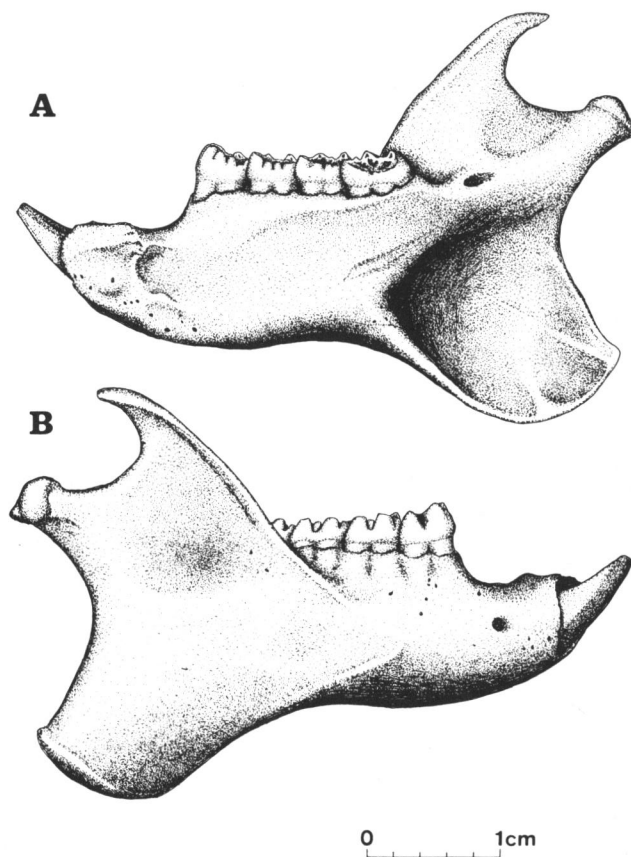


Fig. 89. Right mandible with I, P_4 , M_1 , M_2 and M_3 of *Petaurista leucogenys* from the Holocene horizons of Kannondo Cave Site (HUA-K00673). A, lingual view; B, buccal view.

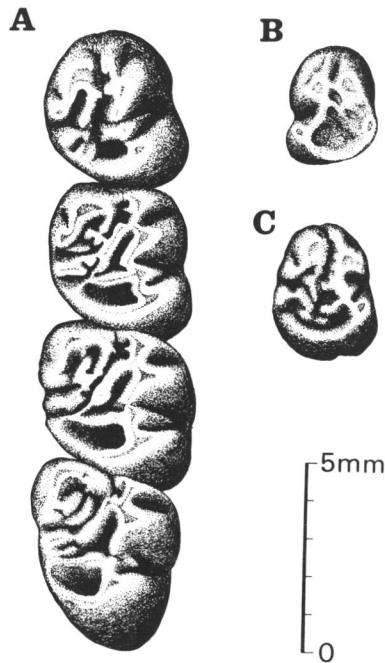


Fig. 90. *Petaurista leucogenys*. Occlusal view of the lower cheek teeth from Kannondo Cave Site. A, right P₄, M₁, M₂ and M₃ from Horizon G (HUA-K00618); B, left dP₄ from Horizon C (HUA-K00644); C, right dP₄ from the upper part of Horizon M (HUA-K00596).

of Horizon M of the same site (HUA-K00596). The latter specimen is somewhat larger and has a more complicate pattern than the former (Fig. 90). However these differences can be interpreted as intraspecific variation.

The occlusal outline of dP₄ is oval. The buccal ridge is formed by the lophate connection of the paraconid, protoconid, mesoconid and hypoconid. The paraconid is small, but can be recognized as an independent cusp in HUA-K00596. In HUA-K00644, however, it is inconspicuous and represented by only an anterior extension of the ridge from the protoconid. The buccal face of the paraconid is strongly concave in the former specimen, but slightly concave in the latter specimen. A short ridge branches off postero-lingually from the buccal ridge between the protoconid and mesoconid in both specimens. The hypolophid extends lingually from the mesoconid in HUA-K00596, while it is absent and the mesoconid is inconspicuous in HUA-K00644. The hypoflexid is wide antero-posteriorly, and opens buccally. The postero-lophid extends lingually from the hypoconid to form the posterior wall of the crown. It reaches the entoconid in HUA-00644, but not in the HUA-K00596.

The metaconid is the largest cusp in the crown. It is separated from the protoconid by a longitudinal central valley in HUA-K00596, but is connected with the protoconid by a short transverse ridge in HUA-K00644. The anterolophid is absent. The mesostylid is small and connected with the metaconid by a short ridge (r4 in Fig. 74). Another ridge from the metaconid runs posteriorly to reach the centre of the crown.

In HUA-K00596, a ridge extends postero-buccally from the entoconid to the centre of the talonid basin remnant. It seems to correspond to the lingual half of the hypolophid. In

HUA-K00644, however, this ridge as well as the hypolophid are absent, so that the talonid basin remnant is confluent with the metafossettid to form a broad basin (true talonid basin). The floor of this basin is somewhat rugose.

dP₄ is anchored by two thick roots. The anterior root extends antero-inferiorly, while the posterior one extends postero-inferiorly.

*P*₄ —

The occlusal outline is oval but broader than that of dP₄. The occlusal pattern is fundamentally similar to that of dP₄, but less complicate and variable than those of the molars.

The paraconid is much smaller than the protoconid, and connected with the latter cusp by a short longitudinal ridge. A narrow valley is formed on the buccal side of this ridge, and it opens anteriorly. The protoconid is elongated antero-posteriorly (somewhat diagonally), so that its postero-lingual end reaches the mesoconid. In slightly worn specimens, however, the former cusp is barely separated from the latter by a narrow transverse notch. The mesoconid is connected with the hypoconid by a slender ridge. The hypolophid begins at the lingual side of the mesoconid, and extends lingually. It sometimes terminates in the middle of the crown, but sometimes elongates more lingually to connect with the entoconid and/or posterolophid. The posterolophid forms the posterior wall of the crown, and sometimes reaches the entoconid.

The metaconid is a large cusp which rivals the protoconid in size. It is crescentic in occlusal view. The anterolophid is not recognizable as in dP₄. From the metaconid, two ridges parallelly extends postero-lingually. The lingual one (r₄ in Fig. 74) reaches the mesostylid, while the buccal one (r₁+r₂+r₃ in Fig. 74) sometimes reaches the entoconid, or sometimes interrupts near this cusp. The entoconid is nearly as large as the mesostylid. Its variation in the connection with the surrounding ridges (the buccal ridge from the metaconid, hypolophid and posterolophid) is analysed in the next section.

*M*₁ —

The outline is a broad rectangle with round corners. The occlusal pattern is complicated by several longitudinal, diagonal and transverse ridges, although the basic structure is equivalent to that of P₄.

The paraconid, protoconid, mesoconid and hypoconid are connected with each other to form a high and continuous ridge on the buccal side of the crown. This ridge (buccal ridge) is zigzag in occlusal view owing to the deep intrusions of two buccal valleys. The anterior valley between the paraconid and protoconid opens antero-buccally, while the posterior one (hypoflexid) opens buccally and is divided into two parts by the mesoconid. The paraconid is sometimes connected with the anterolophid by a short transverse ridge, or sometimes separated from the anterolophid by a median groove. r₁ branches off from the buccal ridge immediately anterior to the protoconid, and extends postero-lingually. A short branch sometimes projects lingually from the buccal ridge between the protoconid and mesoconid. Its lingual end rarely reaches r₁. The hypolophid runs transversely from the mesoconid, and separates the metafossettid from the talonid basin remnant. The posterior wall of the crown is formed by the hypoconid and posterolophid as in dP₄ and P₄.

The structure of the metaconid-metastylid chaos is complicate and highly variable. The

anterolophid is observable but short. The metaconid is equal to or slightly larger than the protoconid. r_2 extends posteriorly from the anterolophid or the buccal part of the metaconid. It sometimes reaches r_1 or the mesostylid, or is sometimes isolated from both of them. r_3 runs posteriorly from the metaconid. In a few specimens, however, it is separated from the metaconid. The posterior end of this ridge sometimes reaches r_2 or even r_1 , while it is sometimes isolated from any ridge or cusp. In a few specimens, r_3 is divided into two short ridges. The metaconid is almost always connected with the mesostylid by r_4 . This ridge is absent from only one specimen among the observed materials. The detailed analysis of such variation is given in the next section.

The entoconid is small and low. It is nearly as large as the mesostylid as in P_4 . In some specimens, it is isolated from r_1 , the hypolophid and posterolophid. In other specimens, however, it is connected with one or two, or all of these ridges. Such variation is also analysed in the next section.

In addition to the above-mentioned features, the minor modifications of cusps and ridges are sometimes observed. They are slight interruptions of the ridges, and weak crenulations of the ridges and cusps. They make the occlusal pattern more complicate.

M_1 always has four roots. The postero-buccal root is the largest of the four, but others have nearly the same size.

M₂ and M₃ —

The occlusal outline of M_2 is similar to that of M_1 , but rather approaches a trapezoid by the posterior extension of the postero-buccal corner. This extension is more advanced in M_3 so that its outline becomes triangular. The occlusal patterns of M_2 and M_3 are basically identical with that of M_1 . However the following minor differences are also observable:

1. The valley between the paraconid and protoconid opens buccally in M_2 and M_3 , but antero-buccally in M_1 .
2. The anterolophids of M_2 and M_3 are more elongated than that of M_1 .
3. The frequency distributions of the morphotypes of the metaconid-metastylid chaos and entoconid are different among these molars (they are discussed in the next section).

Both M_2 and M_3 have four roots. Of these, the postero-buccal one is the largest. In M_2 , the antero-lingual root is slightly larger than the antero-buccal and postero-lingual roots which have nearly the same size. In M_3 , however, the first root is decidedly larger than the last two which are also nearly equal in size. The relative position of the two lingual roots of M_3 is more anterior than those of M_1 and M_2 . A rudimentary rootlet is rarely observed between the two anterior roots in M_2 (Fig. 85) and between the two posterior roots in M_3 .

Morphological analysis of the lower molars

Variation in the metaconid-metastylid chaos —

In order to analyse the variation, the following eight morphotypes are recognized (Table 23).

Morphotype I: The posterior ends of r_2 and r_3 never reach r_1 and the mesostylid. r_2 and r_3 are usually independent, but rarely merged into a single ridge.

Morphotype II: The posterior end of r_2 is separated from r_1 , but that of r_3 reaches the mesostylid. An additional modification is sometimes recognized, where r_3 is bifurcated posteriorly and its two

branches reach the mesostylid and entoconid respectively.

Morphotype III: The posterior ends of r2 and r3 are separated from r1. On the other hand, r2 reaches the mesostylid, but r3 is separated from r2 and the mesostylid.

Morphotype IV: r2 and r3 are separated from r1. However they are connected posteriorly with each other, and reach the mesostylid.

Morphotype V: The posterior end of r2 reaches r1. However neither r3 nor r4 are present. There are traces of a ridge between r1 and the mesostylid which are interrupted.

Morphotype VI: The posterior end of r2 reaches r1, but that of r3 is separated from r1. r3 sometimes connects with the mesostylid.

Morphotype VII: The posterior end of r3 reaches r1, but that of r2 is separated from r1. In addition to these characters, a transverse ridge is rarely observed between r1 and the mesostylid.

Morphotype VIII: The posterior ends of r2 and r3 reach r1.

In the morphotypes I, II, III and IV, the lingual flexid extends antero-buccally to form a long diagonal valley along r1, and usually opens anteriorly between the paraconid and anterolophid. In other morphotypes, however, this valley is blocked by r2 and/or r3, and divided into two or three parts.

The specimen numbers belonging to each morphotype are shown in Table 23. In M₁, the morphotype VIII is most frequently found (37.1%), and the morphotypes VII and VI also abundantly occur (28.6 and 17.1% respectively). The similar tendency is observed in M₂, where the morphotypes VIII and VI are abundantly observed (37.5 and 25.0% respectively).

Table 23. Morphological variation in the metaconid-metastylid chaos of the lower molars of *Petaurista leucogenys*. For detailed explanation of each morphotype see text. The numbers of the specimens belonging to each morphotype are tabulated. m, mesostylid; med, metaconid; pad, paraconid; prd, protoconid.

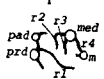
KIND OF TOOTH / FOSSIL LOCALITY	MORPHOTYPES OF METACONID-METASTYLID CHAOS								TOTAL
	I	II	III	IV	V	VI	VII	VIII	
									
M ₁									
Ojika-do Cave	0	0	0	0	0	0	1	1	2
Ninjinkubo First Cave	0	0	0	0	0	0	1	0	1
Anagami Site	0	0	0	0	0	0	0	1	1
Tanuki-ana Cave	0	0	0	0	0	1	0	0	1
Kannondo Site (Holocene)	3	1	1	0	1	5	6	10	27
Suse Quarry (East Fissure)	0	0	0	0	0	0	0	1	1
Kannondo Site (Late Pleist.)	0	0	0	0	0	0	1	1	2
M ₂									
Ojika-do Cave	0	0	0	0	0	0	0	1	1
Tanuki-ana Cave	0	0	0	0	0	2	1	1	4
Kannondo Site (Holocene)	4	0	1	3	0	6	3	8	25
Suse Quarry (East Fissure)	0	0	0	0	0	0	0	1	1
Kannondo Site (Late Pleist.)	0	0	0	0	0	0	0	1	1
M ₃									
Tanuki-ana Cave	0	1	0	0	0	0	0	0	1
Kannondo Site (Holocene)	3	0	5	4	0	3	1	0	16
Suse Quarry (East Fissure)	0	0	0	0	0	1	0	0	1
Kannondo Site (Late Pleist.)	0	0	0	0	0	1	0	1	2
Loc. 3 of Ube Kosan Quarry	0	0	1	0	0	0	0	0	1

Table 24. Variation in the connection of the entoconid with the surrounding ridges in the lower cheek teeth of *Petaurista leucogenys*. For detailed explanation of each morphotype see text. The numbers of the specimens belonging to each morphotype are shown. end, entoconid; h, hypolophid; hyd, hypoconid; msd, mesoconid; p, posterolophid; prd, protoconid.

KIND OF TOOTH / FOSSIL LOCALITY	MORPHOTYPES OF RIDGES AROUND ENTOCONID								TOTAL
	A	B	C	D	E	F	G	H	
									
P₄									
Tanuki-ana Cave	0	0	0	0	0	0	0	2	2
Kannondo Site (Holocene)	6	1	2	6	0	2	3	1	21
M₁									
Ojika-do Cave	0	1	1	0	0	0	0	0	2
Ninjinkubo First Cave	0	0	1	0	0	1	0	0	2
Anagami Site	0	0	1	0	0	0	0	0	1
Tanuki-ana Cave	1	0	0	0	0	0	0	0	1
Kannondo Site (Holocene)	3	2	7	2	0	10	0	4	28
Suse Quarry (East Fissure)	0	0	0	0	0	1	0	0	1
Kannondo Site (Late Pleist.)	0	0	0	0	0	1	0	0	1
M₂									
Ojika-do Cave	1	0	0	0	0	0	0	0	1
Ninjinkubo First Cave	0	0	0	0	0	1	0	0	1
Tanuki-ana Cave	1	1	0	0	0	0	1	0	3
Kannondo Site (Holocene)	7	3	3	1	1	6	0	4	25
Suse Quarry (East Fissure)	0	0	0	0	0	1	0	0	1
Kannondo Site (Late Pleist.)	0	1	0	0	0	0	0	0	1
M₃									
Ninjinkubo First Cave	0	1	0	0	0	0	0	0	1
Tanuki-ana Cave	0	0	0	0	0	0	0	1	1
Kannondo Site (Holocene)	2	2	0	0	0	1	1	11	17
Suse Quarry (East Fissure)	0	0	0	0	0	0	0	1	1
Kannondo Site (Late Pleist.)	0	0	0	0	0	1	0	1	2
Loc. 3 of Ube Kusan Quarry	0	0	0	0	0	0	0	1	1

On the other hand, in M^3 , the morphotypes VII and VIII are rare (4.8% each), but the morphotypes III, IV and VI are rather frequently found (28.6, 19.0 and 23.8% respectively).

Variation of the entoconid —

The variation in the connection of the entoconid with the surrounding ridges is analysed by recognizing the following eight morphotypes (Table 24).

Morphotype A: The entoconid is separated from r1, the hypolophid and posterolophid. The lingual ends of the last two ridges are connected with each other.

Morphotype B: The entoconid is connected with r1, but separated from the hypolophid and posterolophid. The lingual ends of the last two ridges are connected with or separated from each other. In P_4 , this morphotype is indistinguishable from the morphotype E, because r1, r2 and r3 are considered to be merged into a single ridge (the buccal ridge from the metaconid).

Morphotype C: The entoconid is connected with the hypolophid, but separated from r1 and the posterolophid.

Morphotype D: The entoconid is connected with the posterolophid, but separated from r1 and the hypolophid. The lingual ends of the last two ridges are connected with, or separated from each other.

Morphotype E: The entoconid is connected with r3, but separated from r1, the hypolophid and

posterolophid. These three ridges are connected with each other at their lingual ends.

Morphotype F: The entoconid is connected with r1 and the hypolophid, but separated from the posterolophid. In most specimens, the hypolophid is completely separated from the posterolophid by the talonid basin remnant. In a few specimens, however, a weak ridge is formed between the lingual end of the posterolophid and the middle of the hypolophid.

Morphotype G: The entoconid is connected with the hypolophid and posterolophid, but separated from r1.

Morphotype H: The entoconid is connected with r1, the hypolophid and posterolophid.

The numbers of the specimens belonging to each morphotype are given in Table 24. In P₄, all the morphotypes are observed (excepting the morphotype E which is equivalent to B in this tooth). The frequencies of the morphotypes A and D are highest (27.3% each). In M₁, the morphotypes E and G are absent. Among other six morphotypes, F is most abundantly found (36.1%), and C is the second (27.8%). In M₂, all the morphotypes are observed. Among them, the morphotypes F and A abundantly occur (28.1 and 25.0% respectively), but D, E and G are rare (3.1% each). In M₃, the morphotypes C, D and E are absent. Among other five morphotypes, the frequency of H is highest (65.2%), while those of A, B, F and G are much lower (4.3–13.0%).

Measurements

The measurements of the mandibles and cheek teeth are shown in Tables 25–27. The relationship between the length and width of the lower cheek teeth is figured in the scatter diagram (Fig. 91).

These data indicate that the Holocene materials have wide ranges of variation in size, and are generally smaller than the Late and Middle Pleistocene materials. In spite of the scarcity of the latter materials, these size differences can be interpreted as intraspecific, because the larger variants within the Holocene materials have nearly the same size as or sometimes exceeds the Late and Middle Pleistocene materials, and there seem to be no significant differences in dental pattern among the materials with different geological ages.

Comparisons

The dental and osteological characters of the present fossils described above are well coincident with those of the recent specimens of *P. leucogenys* collected from Honshu. Moreover they are distinguishable from those of other living and fossil species of *Petaurista* as mentioned below. Accordingly the present fossils can be identified as *P. leucogenys*.

Comparisons with the living species of Petaurista —

Other than *P. leucogenys*, the following five living species of *Petaurista* are known:

Petaurista alborufus (MILNE-EDWARDS)

Petaurista elegans (MULLER)

Petaurista magnificus (HODGSON)

Petaurista petaurista (PALLAS)

Petaurista xanthotis (MILNE-EDWARDS)

Although several authors have regarded *P. xanthotis* as a subspecies of *P. leucogenys*, McKENNA (1962) treated it as a distinct species. The present author agrees with McKENNA's opinion,

Table 25. Measurements of the mandibles of *Petaurista leucogenys* in mm. The numbers on the left side correspond to those in Fig. 72. UNS, unnumbered specimen (* SOTSUKA Collection; ** MATSUHASHI Collection); $\pm$ approximate value.

	Ojika-do Cave		Ninjinkubo First Cave			Kannondo Cave Site (Holocene horizons)												Horizon B		
						Horizon unknown												Horizon A		
	UNS*	UNS*	UNS*	UNS*	UNS*	HUA-K 00673	HUA-K 00679	HUA-K 00680	HUA-K 00678	HUA-K 00674	HUA-K 00675	HUA-K 00676	HUA-K 00682	HUA-K 00677	HUA-K 00665	HUA-K 00663	HUA-K 00664			
1. Total length of the mandible (id to goc)	—	—	—	—	—	42.83	—	—	—	—	—	—	—	—	—	—	—	41.15		
2. Ditto (id to the condyle)	—	—	41.65	42.09 $\pm$	—	44.06	—	40.39	—	—	—	—	—	—	42.51	43.57	43.25			
3. Length from the tip of the incisor to the condyle	—	—	44.61	45.61	45.36	46.48	—	45.19	—	—	—	—	—	—	45.66	—	45.91			
4. Length of the horizontal ramus	—	—	25.50	25.72 $\pm$	—	27.14	27.88	26.20	—	27.49	—	25.89	—	—	26.70	26.75	26.41			
5. Length of the diastema	—	—	8.06	9.12 $\pm$	—	10.15	9.74	—	—	10.17	—	9.35	—	—	10.04	10.04	9.38			
6. Length of the ascending ramus (the posterior border of M ₃ to the condyle)	16.89	16.44	16.39	16.29	16.86	16.98	—	16.33	—	—	—	—	15.87	16.94	16.67	17.09	17.31			
7. Ditto (the posterior border of M ₃ to goc)	20.55	19.57	—	—	19.71	20.37	—	—	—	—	—	18.36	—	—	—	—	18.70			
8. Height of the ascending ramus (gov to the highest point of the condyle)	26.53	25.70	—	25.01	25.48	25.87	—	—	—	—	—	—	—	—	—	26.20	—			
9. Ditto (cr to the most upper point of the lower border of the ascending ramus)	25.79	27.77	26.27	27.29	26.19	28.12	—	26.73	—	—	—	—	—	—	—	27.20	27.75			
10. Ditto (gov to the mandibular incision)	24.29	23.89	—	23.28	23.97	24.16	—	—	—	—	—	—	—	—	—	24.02	—			
11. Length of the mandibular incision	12.98	11.71	12.34	11.07	11.67	11.15	—	11.44	—	—	—	—	12.10	—	—	10.85	11.38			
12. Height of the horizontal ramus at P ₄	11.47	11.22	10.67	10.40	11.17	11.54	—	10.69	—	—	11.42	10.53	—	10.91	11.56	10.80	10.89			
13. Minimum height of the horizontal ramus	10.87	10.60	10.18	9.89	9.84	10.99	—	9.93	10.49 $\pm$	—	—	9.94	—	10.41	11.10	10.42	10.16			
14. Maximum thickness of the horizontal ramus	6.13	6.33	6.72	6.39	5.95	6.21	6.75	6.02	—	6.42	—	5.87	—	6.68	6.34	6.30	6.37			
15. Length of the cheek tooth row (P ₄ to M ₃) at the crowns	—	—	—	—	—	16.05	—	—	—	16.22	16.22	15.31	—	16.18	16.20	16.02	—			
16. Ditto at the alveoli	16.72	17.43	16.96	16.95	17.07	16.95	17.55	17.41 $\pm$	—	17.45	17.27 $\pm$	16.64	17.13	16.99	16.62	16.77	16.79			
17. Length of the molar row (M ₁ to M ₂) at the crowns	—	—	—	—	12.01	12.27	—	—	13.16	12.26	12.15	11.62	—	12.46	12.31	12.37	—			
18. Ditto at the alveoli	12.27	12.76	12.63	12.98	12.31	12.57	12.74	12.49	13.49	13.10	12.69	12.43	13.06	13.07	12.56	12.94	12.63			

Table 25. (Continued)

	Kannondo Cave Site										(Holocene horizons)										Suse (East Fissure)		Kannondo
	Horizon C								Horizon D	Horizon E	Horizon F		Horizon G			Horizon H	Horizon I			UNS**	Horizon N		
	HUA-K 00644	HUA-K 00642	HUA-K 00646	HUA-K 00645	HUA-K 00648	HUA-K 00649	HUA-K 00643	HUA-K 00621	HUA-K 00647	HUA-K 00634	HUA-K 00631	HUA-K 00629	HUA-K 00628	HUA-K 00618	HUA-K 00619	HUA-K 00620	HUA-K 00609	HUA-K 00600	HUA-K 00601		HUA-K 00602	HUA-K 04148	
1.	—	—	—	—	—	—	42.45	—	—	42.97	—	—	40.61	—	—	—	—	—	—	—	—	—	
2.	40.50	—	—	44.64	—	—	43.52	—	—	44.50	—	—	41.70	44.76	44.94	—	—	—	—	—	—	42.19±	
3.	43.35	—	—	47.28	—	—	—	—	—	46.72	—	—	44.59	—	—	46.76	—	—	—	—	—	44.67	
4.	25.69	—	—	27.31	—	—	27.20	—	—	27.22	—	—	25.65	27.62	27.42	—	—	—	—	27.92	—	27.02±	
5.	9.02±	—	—	10.56	—	—	9.87	—	—	10.15	—	—	8.51	10.19	10.29	—	—	—	—	9.35±	—	—	
6.	16.84	16.86	16.99	17.53	14.86	—	16.71	—	16.64	17.29	17.64	—	16.45	17.45	17.60	17.07	16.79	16.87	17.60	—	—	15.70	
7.	—	—	20.15	20.02	—	—	19.62	—	20.04	19.98	—	—	19.50	—	—	—	—	—	—	—	—	—	
8.	28.14	—	25.19	25.09	—	—	25.22	—	24.56	—	—	—	25.34	—	—	—	—	—	—	—	—	—	
9.	25.23	—	27.59	—	—	—	—	—	29.07	28.21	—	—	26.77	28.43	—	—	27.30	—	—	—	—	—	
10.	20.91	—	24.10	23.82	—	—	23.17	—	23.66	—	—	—	23.76	—	—	—	—	—	—	—	—	—	
11.	10.65	—	11.36	—	—	—	—	—	10.88	11.80	—	—	12.56	12.07	—	—	12.00	—	—	—	—	—	
12.	10.18	11.59	11.23	10.76	10.36	—	11.14	10.63	10.75	10.81	—	10.02±	10.62	10.98	11.05	11.05	—	—	11.25	11.71	11.48	—	
13.	10.18	10.62	10.46	10.27	9.45	10.18	9.99	10.23	10.10	10.02	11.30	10.66	10.28	10.31	10.28	10.47	10.87	10.91±	10.50	—	11.31	10.10	
14.	6.15	6.87	5.95	6.51	5.58	—	5.92	6.02	6.33	6.65	—	5.72	6.68	5.77	6.29	6.57	—	—	6.06	6.50	6.58	6.53	
15.	—	16.11	—	—	—	—	—	—	—	—	16.06	—	—	16.24	—	—	—	17.10	—	—	—	—	
16.	16.92	17.11	16.25	16.82	17.97±	17.88	16.86	17.00	17.24	16.90	17.72	17.65	16.97	17.16	16.86	17.36	17.02	17.68	17.47	18.19±	17.42	—	
17.	—	12.35	—	—	—	—	—	—	—	—	12.08	—	—	12.30	—	12.23	—	12.74	—	13.19	12.18	—	
18.	12.68	12.78	12.17	12.70	13.17	13.22	12.82	12.92	12.74	12.84	12.61	13.06	12.71	12.60	12.82	12.64	12.63	12.95	12.39	13.28	12.46	13.41±	

Table 26. Measurements of the upper cheek teeth of *Petaurista leucogenys* in mm.

LOCALITY AND SPECIMEN NUMBER	dP ⁴		P ⁴		M ¹		M ²		M ³	
	LENGTH	WIDTH	LENGTH	WIDTH	LENGTH	WIDTH	LENGTH	WIDTH	LENGTH	WIDTH
HOLOCENE										
Anagami Site										
HUA-A00004	—	—	—	—	3.62	—	—	—	—	—
HUA-A00001	—	—	—	—	—	—	—	—	3.56	4.59
Tanuki-ana Cave										
ASM 700024	3.59	3.59	—	—	—	—	—	—	—	—
ASM 700025	3.24±	3.45	—	—	—	—	—	—	—	—
ASM 700026	—	—	—	—	3.54	5.09	—	—	—	—
ASM 700030	—	—	—	—	—	—	—	—	3.48	4.57
ASM 700020	—	—	—	—	3.64	4.85	—	—	—	—
Domen Cave Site										
HUA-D00001	—	—	4.10	4.86	—	—	—	—	—	—
Kannondo Site (Holocene horizons)										
HUA-K00667	—	—	4.47	5.08	3.63	4.86	3.63	4.76	3.47	4.37
HUA-K00668	3.70	3.54	—	—	—	—	—	—	—	—
HUA-K00641	—	—	—	—	—	—	—	—	3.33	4.16
HUA-K00635	3.53	3.32	—	—	3.80	4.84	3.68	4.97	—	—
HUA-K00636	—	—	4.46	4.94	3.71	5.16	3.60	4.94	—	—
HUA-K00637	—	—	—	—	3.62	4.99	3.50	4.80	3.31	3.99
HUA-K00633	—	—	—	—	3.45	4.67	—	—	—	—
HUA-K00607	—	—	4.60	5.04	3.84	4.98	3.67	4.92	3.71	4.44
LATE PLEISTOCENE										
Kannondo Site (Late Pleist. horizons)										
HUA-K00594	—	—	—	—	—	—	—	—	3.45	—
HUA-K00587	—	—	—	—	—	—	4.35±	—	—	—
HUA-K00577	—	—	—	—	3.61	4.94	—	—	—	—
MIDDLE PLEISTOCENE										
Locality 3 of Ube Kosan Quarry										
KUJC98062	—	—	—	—	3.95	5.52	—	—	—	—
KUJC98063	—	—	—	—	—	—	—	—	3.74	4.59

Table 27. Measurements of the lower cheek teeth of *Petaurista leucogenys* in mm. UNS, unnumbered specimen (* SOTSUKA Collection; ** MATSUHASHI Collection).

LOCALITY & SPECIMEN NUMBER	LENGTH	WIDTH	LOCALITY & SPECIMEN NUMBER	LENGTH	WIDTH
dP ₄			M ₁ (continued)		
Kannondo Cave Site			Kannondo Site (Holocene horizons)		
Horizon C			Horizon unknown		
HUA-K00644	3.16	2.40	HUA-K00678	4.64	4.07
Horizon M (upper part)			HUA-K00674	4.21	3.53
HUA-K00596	3.57	2.67	HUA-K00675	4.03	3.68
P ₄			HUA-K00676	4.03	3.43
Tanuki-ana Cave (Layer 4)			HUA-K00677	4.18	3.50
ASM 700016	3.86±	3.09	HUA-K00681	4.13	3.39
Kannondo Site (Holocene horizons)			Horizon A		
Horizon unknown			HUA-K00665	4.22	3.66
HUA-K00673	4.13	3.55	Horizon B		
HUA-K00680	4.14	3.48	HUA-K00663	4.00	3.62
HUA-K00674	4.25	3.67	HUA-K00664	4.23	3.70
HUA-K00675	4.28	3.68	Horizon C		
HUA-K00676	3.92	—	HUA-K00644	4.43	3.72
HUA-K00677	4.18	3.24	HUA-K00642	4.28	3.67
HUA-K00681	4.04	3.25	HUA-K00646	3.95	3.42
HUA-K00678	4.36	3.88	HUA-K00645	4.16	3.69
Horizon A			HUA-K00643	4.23	3.68
HUA-K00665	4.26	3.61	HUA-K00647	4.33	3.80
Horizon B			Horizon D		
HUA-K00663	4.13	3.42	HUA-K00634	3.95	3.75
HUA-K00664	4.19	3.46	Horizon E		
Horizon C			HUA-K00631	4.13	3.57
HUA-K00642	4.34	3.40	Horizon F		
HUA-K00646	3.91	3.48	HUA-K00629	4.35	3.79
HUA-K00643	4.39	3.56	Horizon G		
HUA-K00647	4.42	3.62	HUA-K00618	4.17	3.64
Horizon E			HUA-K00619	4.11	3.75
HUA-K00631	4.20	3.46	HUA-K00620	4.07	3.69
Horizon F			Horizon H		
HUA-K00630	4.45	3.52	HUA-K00609	4.14	3.53
HUA-K00628	4.65	3.12	Horizon I		
Horizon G			HUA-K00600	4.45	3.80
HUA-K00618	4.15	3.59	HUA-K00601	3.81	3.41
HUA-K00619	4.18	3.33	HUA-K00602	4.48	3.91
Horizon I			Suse Quarry (East Fissure)		
HUA-K00600	4.73	3.62	UNS**	4.19	3.84
HUA-K00601	3.82	3.17	Kannondo Site (Late Pleist. horizons)		
M ₁			Horizon O (upper part)		
Ojika-do Cave			HUA-K00581	4.70±	3.93
UNS*	4.25	3.58			
UNS*	4.47	3.71	M ₂		
Ninjinkubo First Cave			Ojika-do Cave		
UNS*	4.44	3.68	UNS*	4.65	4.07
UNS*	4.23	3.54	Ninjinkubo First Cave		
Anagami Rockshelter Site			UNS*	4.29	3.90
HUA-A00007	4.34	3.59	Tanuki-ana Cave		
Tanuki-ana Cave (Layer 2)			Layer 2		
ASM 700033	4.13	3.62	ASM 700034	4.34±	3.95±
Kannondo Site (Holocene horizons)			ASM 700019	4.44	3.98
Horizon unknown			Layer 4		
HUA-K00673	4.29	3.94	ASM 700017	4.36	3.62
HUA-K00679	4.00	3.73	ASM 700018	4.63	3.60
HUA-K00686	4.10	3.38	Kannondo Site (Holocene horizons)		
HUA-K00680	4.27	3.79	Horizon unknown		
			HUA-K00673	4.81	4.19
			HUA-K00680	4.47	4.06
			HUA-K00678	5.18	4.31

Table 27. (Continued)

LOCALITY & SPECIMEN NUMBER	LENGTH	WIDTH	LOCALITY & SPECIMEN NUMBER	LENGTH	WIDTH
M ₂ (continued)			M ₃		
Kannondo Site (Holocene horizons)			Ninjinkubo First Cave		
Horizon unknown			UNS*	4.77	3.72
HUA-K00674	4.56	4.14	Tanuki-ana Cave (Layer 2)		
HUA-K00675	4.47	4.12	ASM 700035	5.12	3.91
HUA-K00676	4.84	4.41	Kannondo Site (Holocene horizons)		
HUA-K00677	4.40	4.08	Horizon unknown		
Horizon A			HUA-K00673	5.00	4.20
HUA-K00665	4.67	4.01	HUA-K00674	5.02	4.21
Horizon B			HUA-K00675	5.16	4.21
HUA-K00663	4.72	4.01	HUA-K00676	4.82	3.88
HUA-K00664	4.45	4.14	HUA-K00677	5.37	4.30
Horizon C			Horizon A		
HUA-K00642	4.50	4.10	HUA-K00665	5.03	4.05
HUA-K00658	4.54	3.52	Horizon B		
HUA-K00646	4.37	3.77	HUA-K00663	5.38	4.19
HUA-K00645	4.35	3.85	Horizon C		
HUA-K00643	4.68	4.06	HUA-K00642	5.00	3.92
HUA-K00647	4.52	4.23	HUA-K00660	5.09	4.05
HUA-K00659	4.61	4.12	HUA-K00661	5.18	4.16
Horizon D			Horizon E		
HUA-K00634	4.38	3.94	HUA-K00631	5.09	3.94
Horizon E			Horizon G		
HUA-K00631	4.60	3.92	HUA-K00618	4.93	4.00
Horizon G			HUA-K00624	5.05	3.85
HUA-K00618	4.40	4.04	HUA-K00620	5.18	4.00
HUA-K00619	4.48	4.03	Horizon I		
HUA-K00620	4.37	4.11	HUA-K00600	5.05	4.42
Horizon I			HUA-K00602	5.41	4.36
HUA-K00605	4.61	4.02	Suse Quarry (East Fissure)		
HUA-K00600	4.63	4.34±	UNS**	5.07	3.83
HUA-K00601	4.20	3.94	Kannondo Site (Late Pleist. horizons)		
HUA-K00602	4.79	4.30	Horizon M (lower part)		
Suse Quarry (East Fissure)			HUA-K00589	5.44	4.47±
UNS**	4.62	3.98	Horizon N		
Kannondo Site (Late Pleist. horizons)			HUA-K00586	5.31	4.37±
Horizon M (upper part)			Horizon O (upper part)		
HUA-K00588	—	4.66±	HUA-K00583	—	4.34
Horizon O (upper part)			Horizon P		
HUA-K00582	4.88	4.38	HUA-K00570	5.16	3.97±

because *P. leucogenys* is considerably different from *P. xanthotis* in dental characters.

Because the comparable data on *P. magnificus* distributed in Tibet, Nepal and Sikkim are not available, the present fossils are compared with other four species. On the basis of the biometrical data provided by MEIN (1970), *P. alborufus* is larger than the present fossils, while *P. elegans* is smaller. On the other hand, *P. petaurista* and *P. xanthotis* approximate the present fossils in size. However they can be distinguished from the present fossils in the patterns of cheek teeth.

In comparison with the figures of the cheek teeth of *P. petaurista* given by STEHLIN and SCHAUB (1951) and SULIMSKI (1964), the present fossils differ in having less developed posteroloph in the upper cheek teeth and relatively larger M³. In addition to these, the endoloph of the upper cheek teeth runs antero-posteriorly to make a gentle wavy line in the present fossils (but it runs somewhat diagonally to make a straight line in *P. elegans*), and the transverse ridge which branches lingually from the buccal ridge between the protoconid and

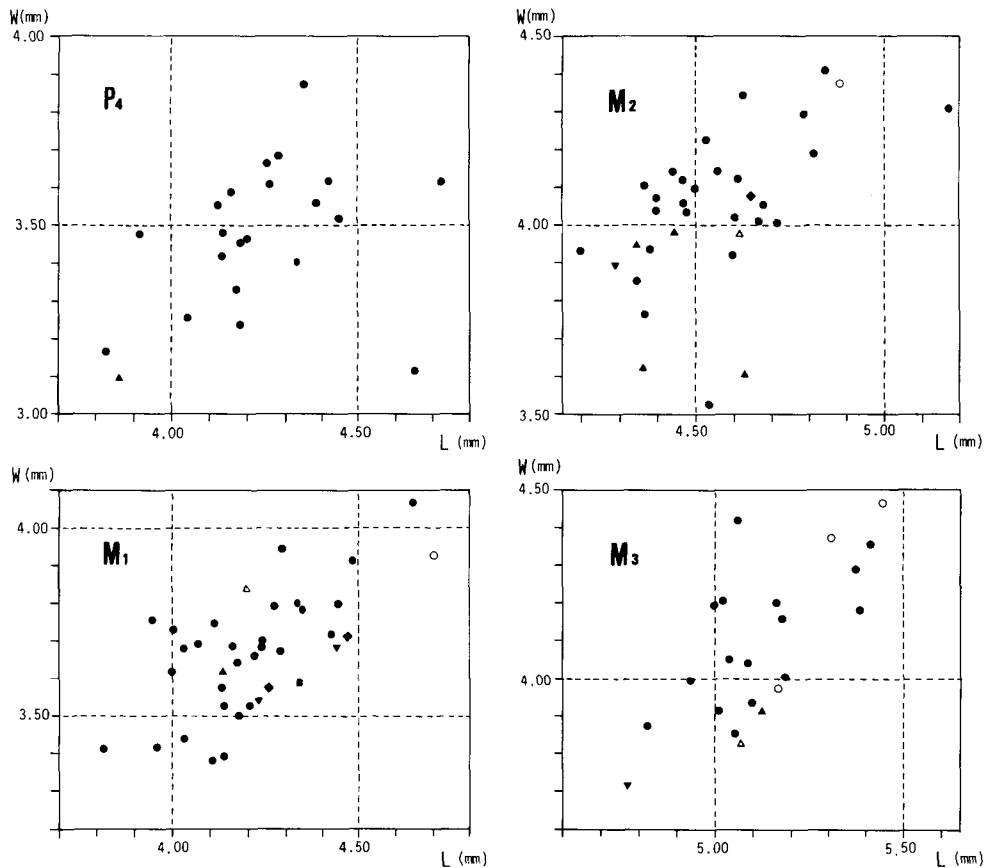


Fig. 91. Scatter diagram showing the relationship between the length and width of the lower cheek teeth of *Petaurista leucogenys*. open symbols, Late Pleistocene materials (○ Late Pleistocene horizons of Kannondo Cave Site; △ East Fissure of Suse Quarry); solid symbols, Holocene materials (● Holocene horizons of Kannondo Cave Site; ▲ Tanuki-ana Cave; ■ Anagami Rockshelter Site; ▼ Ninjinkubo First Cave; ◆ Ojika-do Cave).

mesoconid is weaker in the lower cheek teeth of the present fossils.

The cheek teeth of *P. xanthotis* described and illustrated by McKenna (1962) are considerably different from those of the present fossils. The outlines of the upper cheek teeth are broader and more triangular in *P. xanthotis* than in the present fossils. The anterior cross loph and posteroloph of these teeth are better developed in *P. xanthotis*. The postfossettes on P_4 , M_1 and M_2 are divided into double pits in *P. xanthotis*, but they are a single valley in the present fossils. M_3 of *P. xanthotis* has a simpler pattern, and lacks the posterior cross loph (but present in M_3 of the present fossils). The patterns of the lower cheek teeth of *P. xanthotis* generally resemble those of the present fossils, but the lingual opening of the talonid basin remnant is deeper in the former than in the latter.

Comparisons with the fossils of Petaurista hitherto recorded from Japan —

In 1949, SHIKAMA described a mandible of large flying squirrel from the Upper Kuzui Formation which were referred to *P. cf. leucogenys*. The patterns of the cheek teeth of this specimen are nearly identical with those of the present fossils, but the former is considerably larger than the latter. On the basis of SHIKAMA's measurements, this specimen is larger than the largest variant of the present fossils. However the present author prefers to interpret the size difference as intraspecific rather than interspecific by the following reasons:

- (1) There are no significant differences in dental pattern.
- (2) There seem to be wide ranges of size variation in the living and fossil populations of *P. leucogenys*.
- (3) The postglacial dwarfing seems to be observed in several species of the Japanese mammals. It might take place in the population of this species.

In 1976, KOWALSKI and HASEGAWA described the fossils of *P. leucogenys* from several localities of Japan. Although their description is insufficient, they stated that these fossils did not differ morphologically from the recent comparative materials of *P. leucogenys* and seemed to be of the same size. On the basis of their observation, these fossils are considered to be conspecific with the present fossils. Their measurements of the upper cheek teeth of these fossils are, in fact, approximately coincident with those of the present fossils. Nevertheless the lower cheek teeth of the former as well as those of the recent materials given by the same authors are thoroughly smaller than those of the present fossils. Such size differences may be attributable to the difference in the method of measurements, although the present author could not observe their materials.

Comparisons with the fossil Petaurista from China —

YOUNG (1934) proposed *Pteromys brachyodus* as a new fossil species based on a fragmental mandible with P_4 and damaged M_3 from Locality 1 of Choukoutien. Subsequently, YOUNG and LIU (1950) included this species into *Petaurista*. Although the crowns of the cheek teeth of *P. brachyodus* are as high as those of the present fossils, the former is considerably different from the latter in size and pattern. Namely *P. brachyodus* is smaller than the present fossils. In addition, P_4 of *P. brachyodus* has a simpler pattern, where the mesoconid and hypoconid are poorly developed and the buccal ridge from the metaconid ($r1+r2+r3$) is lacking. As regards the preserved part of M_3 of *P. brachyodus*, however, the pattern resembles that of the present fossils.

In 1950, YOUNG and LIU reported two forms of flying squirrel from Koloshan. They are identified as *Petaurista cf. brachyodus* and *Petaurista sp.* Both forms are considerably different from the present fossils. *P. cf. brachyodus* (Fig. 6b of these authors) is much smaller, and has M_3 with quite different outline and pattern. On the other hand, two specimens of " P^4 " are assigned to *P. sp.* (Fig. 6a of the same authors). These specimens seem not to be P^4 but M_3 . Even if they are referred to M_3 , they are different from the present fossils in having larger size and the following characters: In *P. sp.*, $r1$ extends transversely to reach the mesostylid, while it extends diagonally in the present fossils. Additionally, the transverse ridge which branches lingually from the buccal ridge between the protoconid and mesoconid is better developed in *P. sp.*

Recently, HU and QI (1978) described an isolated M^2 from Lantian which was assigned to *Petaurista* sp. This specimen is near to the present fossils in size. But judging from their figure (Pl. 3, Fig. 14), this form can be distinguished from the present fossils in having broader outline of the crown, and well-developed anterior cross loph which reaches the anteroloph. Moreover it differs from them by the absence of the posterior cross loph.

Consequently none of these Chinese fossils have the characters which indicate the close relationship with the present Japanese fossils or the ancestry of them.

Discussion

Because the Chinese living forms which have been included in *Petaurista leucogenys* as its subspecies seem to be distinct in specific rank from the Japanese one, the recent distribution of *P. leucogenys* is possibly restricted to Honshu, Shikoku and Kyushu. The occurrences of the fossils of this species from these areas indicate that it has inhabited there since the middle Middle Pleistocene. Although allied forms can not be found among the fossils of *Petaurista* hitherto described from North and Central China, the ancestor of *P. leucogenys* possibly immigrated from South China or Southeast Asia. The reason for this inference is the recent concentrative distribution of the species of *Petaurista* in Southeast Asia. It is probable that the ancestral species of the genus arose in this area, and then spread into the adjacent areas. The Middle Pleistocene immigration of mammals from Central and South China to Japan has been suggested by several authors from the fact that *Stegodon orientalis*, a representative elephant of the former areas, are abundantly found in the Middle Pleistocene sediments of Japan. In association with this elephant, the ancestor of *P. leucogenys* was possibly introduced from the southern part of the continent.

The living *P. leucogenys* is an inhabitant of forests as the other species of *Petaurista*. Therefore this species can be regarded as an indicator of sylvan environments. Because the fossils of *P. leucogenys* are found in the middle Middle Pleistocene to Holocene localities of Japan, it can be roughly inferred that the sylvan environments have been predominant in Japan since the middle Middle Pleistocene.

Petaurista sp.

(Fig. 92)

Material—— 1 left M^2 from Layer 2 of Tanuki-ana Cave (ASM 700036).

Diagnosis

Size much smaller than that of *P. leucogenys*; general pattern of M^2 similar to that of *P. leucogenys*, but somewhat simpler; anterior cross loph of M^2 absent; posterolingual diagonal flexus much larger than postfossette in M^2 .

Description

The crown is very slightly worn. The root is not formed owing to the juvenility of the individual. The occlusal outline of the crown is transversely broadly elliptical, and resembles

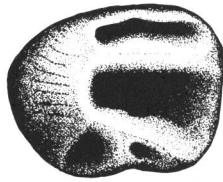


Fig. 92. *Petaurista* sp. Occlusal view of left M^2 from Layer 2 of Tanuki-ana Cave (ASM 700036).

0 1 mm

that of M^2 of *P. leucogenys*.

The parastyle and anteroloph are well merged to form a slender anterior transverse ridge, which meets the endoloph at right angles. The endoloph is the highest part in the crown. There are several faint vertical grooves on its lingual face, but the remarkable groove observed on this face of the cheek teeth of *P. leucogenys* is lacking. The protocone and hypocone are completely fused, so that they are indistinguishable from each other. The protoloph is considerably thick, and runs parallel to the anteroloph. The protoconule is recognizable as a swelling of this ridge. The anterior cross loph is absent. The posterobuccal flexus is much wider than the paraflexus. These valleys become much shallower at their buccal entrances. The floors of the valleys are flattened. The metaloph is thick, but somewhat slenderer than the protoloph. The metaconule is completely fused into this ridge. The posterolingual diagonal flexus is relatively short but wide. It is well separated from the postfossette by the posterior cross loph. The postfossette is a shallow elliptical depression. It is much smaller and shallower than the posterolingual diagonal flexus. The posteroloph is low and indistinct.

Measurements

Length of the crown	2.23 mm
Width of the crown	2.85 mm

Comparisons

On the basis of the measurements of the cheek teeth of *Petaurista leucogenys*, the length of the lower cheek tooth row of the individual which had the present M^2 is approximately estimated to be 9 to 10 mm. This value is considerably smaller than those of such living species as *P. alborufus*, *P. elegans*, *P. leucogenys* and *P. petaurista* given by MEIN (1970). It is also much smaller than that of the living *P. xanthotis*. In addition, the present fossil differs from *P. leucogenys*, *P. petaurista* and *P. xanthotis* in having somewhat simpler pattern and proportionately wider posterolingual diagonal flexus.

In comparison with the fossils of *Petaurista* hitherto described from Japan, the present fossil is decidedly smaller (see the measurements of KOWALSKI and HASEGAWA, 1976, and Table 26 of this paper). On the other hand, the only comparable form among the Chinese fossil *Petaurista* is *P. sp.* from Lantian recorded by HU and QI (1978), because this form is represented by M^2 .

However this form is easily distinguishable from the present fossil by larger size, presence of anterior cross loph, and absence of posterior cross loph.

An extinct genus, *Petauria*, known from the European Pleistocene has the patterns of cheek teeth similar to *Petaurista*. Based on the description and figure provided by KOENIGSWALD (1973), M^2 of *Petauria* resembles the present fossil in having smoothed floor of each valley, wider posterolingual diagonal flexus than postfossette, weak posteroloph, and much wider posterobuccal flexus than paraflexus (about twice or more). However the present fossil clearly differs from M^2 of *Petauria* by the absence of mesostyle, by relatively longer anteroloph and by the hypocone indistinguishable from the protocone. Additionally, the measurements given by DEHM (1962) and MEIN (1970) indicate that the known species of *Petauria* are much larger than the present fossil.

Discussion

Because the specimen described here is most similar to *Petaurista* in tooth pattern among the fossil and living petauristines, it is assigned to *Petaurista*. However it is considerably different from the living species and fossil forms of the genus hitherto described in having remarkably smaller size and several peculiar characters of the pattern. The extreme scarcity of specimen makes the determination of its definite taxonomic position more difficult. The affinity of the present form can not be fully understood, until additional specimens are adequately obtained. It can be said, at least, that this form was coexistent with *P. leucogenys* in Honshu in the Early Holocene.

Genus *Pteromys* CUVIER, 1800

Remarks

The smaller form of the fossil petauristines found in Japan is undoubtedly assigned to the genus *Pteromys* by the coincidence of the osteological and dental characters with the genus. On the other hand, it is readily distinguishable from *Petaurista* and *Petauria* by much simpler patterns of the lower molars as well as by smaller size. The fossil petauristines known from the European Neogene are more or less similar to the present form in dental characters. As these petauristines, MEIN (1970) listed *Miopetaurista*, *Cryptopterus*, *Forsythia*, *Pliopetes*, *Blackia* and *Pliopetaurista*. Subsequently, MEIN's *Miopetaurista* and *Cryptopterus* were emended as *Alvernensia* and *Miopetaurista* respectively by DAXNER-HÖCK and MEIN (1975). Recently BRUIJN *et al.* (1980) added *Aliveria* to these as a new genus. Among these genera, *Pliopetes* and *Blackia* are easily distinguishable from the present form by the clear differences in tooth pattern, especially in having granulate floors of valleys or basins of cheek teeth. *Aliveria* is also easily distinguishable in having cheek teeth with simpler patterns which are rather similar to those of *Sciurus*. The other four genera are closely compared with the present form as follows:

Alvernensia has the following differential characters in the cheek teeth: 1) size larger; 2) each loph more or less crenulated; 3) floor of each valley or basin usually granulated; 4) hypocone strongly developed in upper cheek teeth; 5) P^4 larger than M^1 ; 6) metaloph of M^3 connected with the lingual part of posteroloph; 7) antero-buccal wall of protoconid not

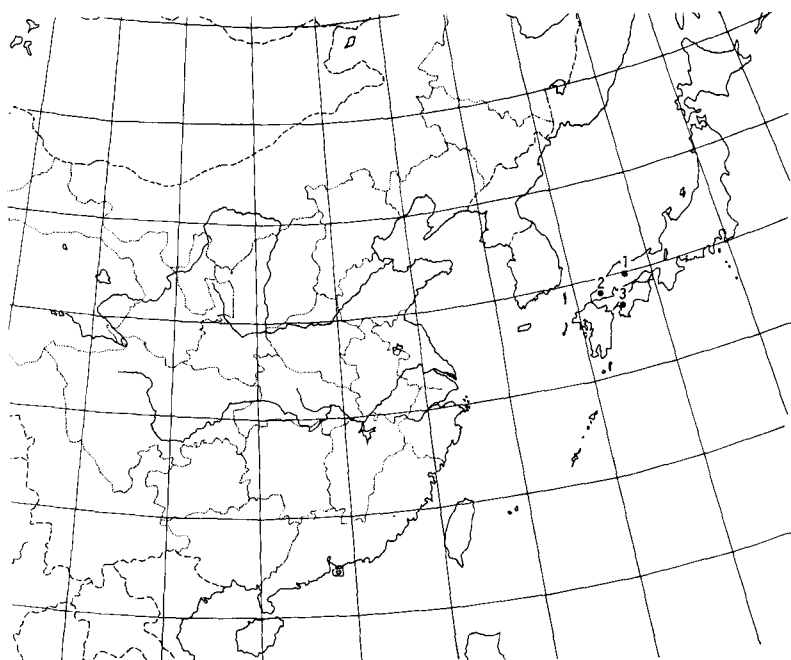


Fig. 93. Fossil localities of *Pteromys* in East Asia. 1, Kannondo Cave Site; 2, Akiyoshi Area (Ando Quarry and Locality 3 of Ube Kosan Quarry); 3, Shikimizu Quarry. For detailed explanation see Table 28.

Table 28. Fossil localities of *Pteromys* in East Asia. The numbers on the left side correspond to those in Fig. 93.

LOCALITY	IDENTIFICATION	REFERENCES
MIDDLE PLEISTOCENE		
2. Ando Quarry	<i>Pteromys</i> cf. <i>volans</i>	Kowalski & Hasegawa (1976)
2. Locality 3 of Ube Kosan Quarry	<i>Pteromys momonga</i>	This paper
LATE PLEISTOCENE		
1. Kannondo Cave Site (Late Pleist. horizons)	<i>Pteromys momonga</i>	Kawamura (1981, 1982), Kawamura et al. (1986); this paper
3. Shikimizu Quarry	<i>Pteromys</i> sp.	Kowalski & Hasegawa (1976)
HOLOCENE		
1. Kannondo Cave Site (Holocene horizons)	<i>Pteromys momonga</i>	This paper

depressed in lower molars.

Miopetaurista (in sense of DAXNER-HÖCK and MEIN) differs from the present form in having the following characters: 1) size much larger; 2) mesostyle present and posteroloph better developed in upper cheek teeth; 3) metaloph continuous and posterior cross loph absent or weak in the same teeth; 4) protoloph and metaloph not converged also in the same teeth; 5) P^4 larger than M^1 ; 6) metaloph absent in M^3 ; 7) mesostylid better developed in lower cheek teeth.

Forsythia is also different in the following characters: 1) posterior cross loph absent or weak in upper cheek teeth; 2) metaloph straighter and more continuous in M^1 and M^2 ; 3) metaloph of M^3 connected with the lingual part of posteroloph; 4) mesostylid well-developed and united with metaconid in lower cheek teeth; 5) hypolophid absent from M_3 .

Pliopetaurista has the following differential characters: 1) posteroloph better developed in upper cheek teeth; 2) mesostyle present in P^4 ; 3) P^4 larger than M^1 ; 4) metaloph absent from M^3 ; 5) mesostylid well-developed in lower cheek teeth, and connected by a ridge to metaconid or to entoconid.

Because these differences are considered to be over generic, the present form is unable to allocate to these genera. However, if remotely compared, it is rather similar to *Alvernensia*, *Pliopetaurista* and *Forsythia* than *Miopetaurista*.

The genus *Pteromys* is composed of the only two Palaearctic species, *P. volans* and *P. momonga*, at the present day. As the circumstance in Europe pointed out by KURTÉN (1968), the fossils of *Pteromys* are rarely recorded from East Asia. In this area, their occurrences are restricted to the Quaternary deposits of Japan (Fig. 93; Table 28). Almost all of them seem to be identifiable as *P. momonga* as discussed below.

***Pteromys momonga* TEMMINCK, 1844**

(Figs. 94, 95)

Pteromys (*Sciuropterus*) *momonga*, TEMMINCK 1844, *Fauna Japonica, Mamm.*, 47–49.

Synonym (living forms) —

Sciuropterus momonga momonga (TEMMINCK) and *S. m. amygdali* THOMAS; KISHIDA 1924, *Honyodobutsu Zukai* (*Monogr. Japanese Mamm.*), 162–163.

Sciuropterus momonga momonga (TEMMINCK & SCHLEGEL) and *S. m. amygdali* THOMAS; KURODA 1940, *Monogr. Japanese Mamm.*, 95–96.

Pteromys volans amygdali (THOMAS); IMAIZUMI 1949, *Nat. Hist. Japanese Mamm.*, 224.

Pteromys momonga TEMMINCK; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palaearctic and Indian Mammals*, 467–468.

Pteromys volans momonga T. & S., *P. v. amygdali* (THOMAS) and *P. v. interventus* (KURODA); KURODA 1953, *Nippon Jurui Zuzetsu* (*Monogr. Japanese Mamm.*), 78.

Pteromys momonga TEMMINCK; IMAIZUMI 1960, *Coloured Illustr. Mamm. Japan*, 120–121.

Pteromys momonga; CORBET 1978, *The Mammals of the Palaearctic Region*, 86–87.

Synonym (fossil forms) —

Pteromys cf. *volans* (LINNAEUS); KOWALSKI and HASEGAWA 1976, *Bull. Nat. Sci. Mus.*, Ser. C, 2, 36; from Ando Quarry.

Pteromys momonga TEMMINCK; KAWAMURA 1981, 1982, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, 4, 69; 5, 60; from Kannondo Cave Site.

Pteromys momonga TEMMINCK; KAWAMURA *et al.* 1986, *Ibid.*, 9, 71; from Kannondo Cave Site.

Materials—

Locality 3 of Ube Kosan Quarry

1 isolated M_2 from Layer 5 (KUJC98066)

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

Horizon O (lower part): 1 fragmental maxilla (K00353); 1 isolated M^1 (K00354); 1 isolated M^3 (K00355); 1 isolated P_4 (K00356); 2 isolated M_1 (K00357, 00358).

Horizon O (upper part): 1 isolated M^1 (K00351); 1 isolated dP_4 (K00352); 2 isolated P_4 (K00348, 00350); 1 isolated M_1 (K00349).

Horizon N: 1 isolated P^4 (K00344); 2 isolated M^1 (K00341, 00343); 1 fragmental mandible with P_4 and M_1 (K00346); 1 isolated M_1 (K00342); 1 isolated M_2 (K00347); 1 isolated M_3 (K00345).

Horizon M (lower part): 1 fragmental mandible (K00340); 1 isolated M_1 (K00333).

Horizon M (upper part): 2 isolated M^1 (K00323, 00335); 1 isolated M^2 (K00336); 1 isolated M^3 (K00332); 1 fragmental mandible (K00324); 1 isolated dP_4 (K00330); 2 isolated P_4 (K00321, 00334); 2 isolated M_1 (K00325, 00326); 7 isolated M_2 (K00322, 00327, 00328, 00331, 00337–00339); 1 isolated M_3 (K00329).

Kannondo Cave Site (Holocene horizon)

Horizon I: 1 mandible with P_4 (HUA-K00689).

Tanuki-ana Cave

Layer 4: 1 isolated M_1 (ASM 700037).

Layer 3: 1 isolated M^1 (ASM 700038).

Diagnosis

The following characters can be added to those given in the key of the Japanese sciurid genera (p. 156): Size generally larger than that of *P. volans*; a short transverse process extending from endoloph into paraflexus mostly absent from upper molars (if present, it is very obsolete); M^3 with posterior cross loph.

Description

The size is smallest among the Japanese sciurids. The cheek teeth are not hypsodont. Their crowns are nearly as high as those of *Petaurista leucogenys* (Fig. 85). Their patterns are rather similar to those of *Sciurus* than *Petaurista*.

Maxilla—

Only one maxillary fragment is available for the present study (HUA-K00353). This specimen is too fragmental to describe in detail. As far as the preserved part is concerned, the alveolar pits for upper molars are nine (three for each molar). The pits of the lingual row is larger than those of the buccal row.

 P^4 —

P^4 is represented by only one specimen (HUA-K00344). The outline of the crown is trapezoid in occlusal view. The protocone is the largest cusp in the crown. A weak but broad ridge projects anteriorly from this cusp, and descends towards the anterior margin of the crown. Near the margin, it turns lingually to form a low additional cusp. The lingual wall of the crown is grooved between this cusp and the protocone. The hypocone is well defined, but much lower than the protocone. This cusp is well united with the posterior wall of the protocone. A weak groove is observed on the lingual wall of the crown between these cusps.

The parastyle is triangular in occlusal view. Because the paraflexus opens both lingually and buccally, the parastyle is well separated from the adjacent lophs and cusps. The

paraflexus is deep and somewhat broadens lingually. The paracone is well fused into the protoloph. This loph gradually descends lingually. The lingual part of the loph is composed of the protoconule, but this cusp is almost indistinguishable. A narrow groove is observed on the lingual end of the anterior face of the protoloph. The posterobuccal flexus is as deep as the paraflexus, but slightly wider than the latter valley. The posterobuccal flexus somewhat tapers lingually.

The metaloph is quite incomplete, and almost interrupted by the posterolingual diagonal flexus and postfossette. This loph begins with a short buccal projection of the protocone. Between the tip of this projection and the metaconule, it is barely represented by a low and narrow ridge which is only slightly higher than the floors of the posterobuccal flexus and posterolingual diagonal flexus. This part of the metaloph is biased anteriorly. The metaconule is well developed and rectangular in occlusal view. Its long axis is considerably oblique to that of the crown. Between this cusp and the metacone, the metaloph is also represented by a low and narrow ridge which is biased anteriorly. This part of the metaloph is much lower than the apexes of the metaconule and metacone, but considerably higher than the floors of the

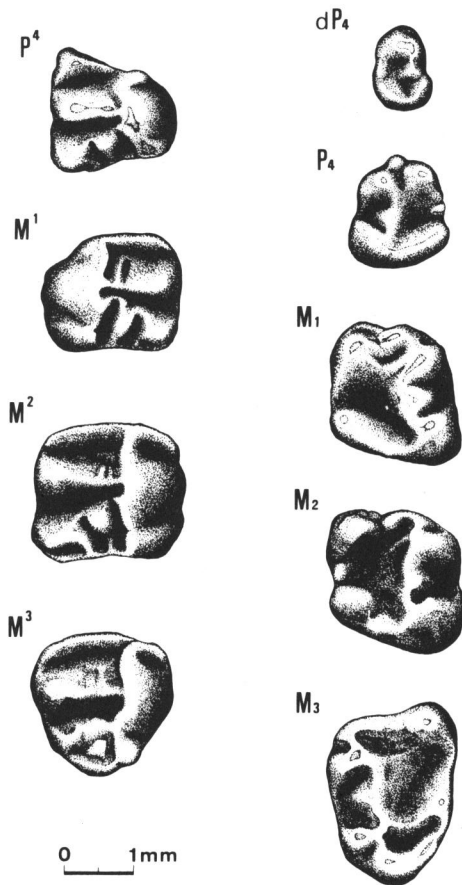


Fig. 94. *Pteromys momonga*. Occlusal view of the cheek teeth from Kannondo Cave Site (P^4 , M^1 , M^2 , M^3 , dP_4 , P_4 , M_1 and M_3) and Locality 3 of Ube Kosan Quarry (M_2). P^4 , right P^4 from Horizon N (HUA-K00344); M^1 , left M^1 from the same horizon (HUA-K00343); M^2 , right M^2 from the upper part of Horizon M (HUA-K00336); M^3 , right M^3 from the same horizon (HUA-K00332); dP_4 , right dP_4 from the same horizon (HUA-K00330); P_4 , left P_4 from the upper part of Horizon O (HUA-K00348); M_1 , right M_1 from Horizon N (HUA-K00346); M_2 , right M_2 from Layer 5 (KUJC98066); M_3 , left M_3 from Horizon N (HUA-K00345).

posterobuccal flexus and postfossette. The metacone is conical, but somewhat elongated transversely. It is much higher and larger than the metaconule. The posterior wall of the metacone is smoothed and not grooved transversely.

The present tooth has three roots. The lingual root below the protocone is nearly as large as the antero-buccal root below the parastyle. The cross sections of these roots are elliptical. The postero-buccal root is almost lost in this specimen.

*M*¹ —

The occlusal outline of the crown is nearly quadrate in occlusal view. The basic structure of the crown is nearly equivalent to that of *P*⁴, but several modifications are also observed.

The protocone is the largest cusp and forms the most part of the endoloph. From the apex of the protocone, this loph descends anteriorly and posteriorly. It meets the anteroloph at right angles. The lingual face of the endoloph in front of the protocone is grooved. In a few specimens, this groove is well-defined so that a ridge is formed along the anterior end of the endoloph as the lingual extension of the anteroloph. In other specimens, this groove is shallower, and such a ridge is indistinct or absent. The hypocone is attached on the posterior face of the protocone to form the posterior end of the endoloph. A shallow groove is observed on the lingual face of the endoloph between these cusps.

The anteroloph is slender and low, and runs along the anterior margin of the crown. The parastyle is represented by a weak swelling at the buccal end of the anteroloph. It is much lower than the paracone. In contrast with *P*⁴, the paraflexus opens only buccally. This valley broadens lingually. Its floor is usually smoothed, but in only one specimen (HUA-K00335) out of six, a small and low protuberance is observed at the lingual end of this floor.

The paracone is the second largest cusp, and as high as the protocone. This cusp is triangular in occlusal view. It is connected with the endoloph by a slender loph (lingual half of the protoloph). From the middle of this loph, the anterior cross loph extends anteriorly towards the bottom of the paraflexus. It is small and slender, but well-defined by the grooves on both sides. The posterobuccal flexus is deeper and narrower than the paraflexus. This valley gradually broadens buccally and opens at the buccal margin of the crown.

The metaloph branches from the endoloph at the apex of the protocone, and extends postero-buccally to the metacone through the metaconule. It shows an inverted "ω" shape in occlusal view. It is extremely slender between the protocone and metaconule, and between the latter and metacone. It also becomes lower in these parts. The metaconule is well-developed, but considerably lower than the protocone. It is also smaller than the hypocone, and shows an elliptical shape elongated antero-posteriorly in occlusal view. The posterior cross loph is observable, but very short. It steeply descends posteriorly. The posteroloph is absent. The metacone is transversely elliptical in occlusal view. It is slightly lower than the metaconule, but higher than the hypocone. There is a small but remarkable depression on the posterior face of the metacone. This depression is never confluent with the postfossette. The postero-lingual diagonal flexus is longer than the postfossette. However these valleys have nearly the same width, and opens posteriorly. The long axes of these valleys are set somewhat obliquely to that of the crown. These valleys are deep, and as deep as the posterobuccal flexus.

M¹ generally has three roots. In only one specimen (HUA-K00323) out of six, however, a very small additional rootlet is observed immediately lingual to the base of the antero-buccal root. The lingual root is much larger than other two roots. The antero-buccal root is slightly smaller than, or as large as the postero-buccal root. The cross sections of these three main roots are round or broadly elliptical.

M² —

M² is represented by a single specimen (HUA-K00336). The occlusal outline and pattern of the crown of this specimen are almost identical with those of M¹. However this specimen also has the following differential characters:

1. The groove on the lingual face of the endoloph in front of the protocone is generally broader and more distinct in this specimen than in M¹.
2. The anterior cross loph is represented by double projections.
3. The metaloph is quite indistinct and low between the protocone and metaconule.
4. The depression on the posterior wall of the metacone is large and forms a transverse groove.
5. The posterior cross loph is slightly longer than in M¹.
6. The posteroloph is recognizable.

Among these characters, 2 and 3 seem to be peculiar to this specimen, and not to be general characters of M².

This specimen has three roots. Their features are identical with those of M¹.

M³ —

M³ is represented by two specimens only (HUA-K00332 and 00355). Because the latter specimen is strongly worn, the pattern of its crown can not be observed. Therefore the following observation is obtained from the former specimen only.

The outline of the crown is broadly obovate in occlusal view. The basic structure of the crown corresponds to that of M¹, but its posterior part is remarkably reduced. The lingual wall of the endoloph is distinctly grooved in front of and behind the protocone as in M². The endoloph turns lingually at its anterior end to form a low and short ridge along the anterior margin of the crown. It is as distinct as in M², but considerably stronger than in M¹. The hypocone is as large as the metaconule, but less developed than in other molars.

The anteroloph is low and gradually descends lingually. The paraflexus is relatively shallow and opens buccally. The paracone is as high as the protocone. The protoloph descends centrally, but much higher than the anteroloph. The anterior and posterior walls of the protoloph are rugose. The anterior cross loph is indistinct, and seems to be represented by a few wrinkles on the anterior wall of the protoloph. The posterobuccal flexus is deeper than the paraflexus, and opens buccally. The metaloph is more continuous than those of M¹ and M². However it is shorter than the protoloph. It retains a constant height from the metacone to its lingual end. The metaconule is represented by a central swelling of this loph. The metacone is poorly developed and very narrow. It is much smaller than the metaconule. Because the posterior cross loph is slightly isolated from the metaconule, it is observed as a low cusp in the valley behind the metaloph which is formed by the union of the posterolingual diagonal flexus and postfossette. This valley opens buccally behind the metacone. The posteroloph is low but distinct. It branches from the endoloph at the hypocone, and extends

along the posterior margin of the crown to reach near the posterior base of the metacone.

M^3 has three roots which are round or broadly elliptical in cross section. The antero-lingual root is slightly larger or as large as the posterior root. The antero-buccal root is much smaller than these roots.

Mandible —

The mental foramen is relatively large. Its posterior border is situated just anterior to the position below the anterior margin of P_4 . The lower and upper masseteric crests are distinct. They meet with each other below the middle of P_4 . The area between the alveoli and ascending ramus is narrow and flattened. The mandibular foramen is large, and opens immediately behind M_3 at the same level as the alveoli. The alveolar pits attain to 14 in number (two for P^4 and four each for other teeth). Their pattern is shown in Fig. 95.

dP₄ —

Only two specimens are available for the present study (HUA-K00330 and 00352). The outline of the crown is ovate in occlusal view. The crown comprises the central vasin (talonid basin) and the cusps which surround the basin.

The protoconid and metaconid is almost merged to form a single anterior cusp. It is the largest and highest cusp in the crown. A faint tubercle on the anterior face of this cusp (somewhat biased buccally) is possibly assigned to paraconid. A ridge extends posteriorly from the anterior cusp to the mesoconid. The latter cusp is small and ridge-like. It is much

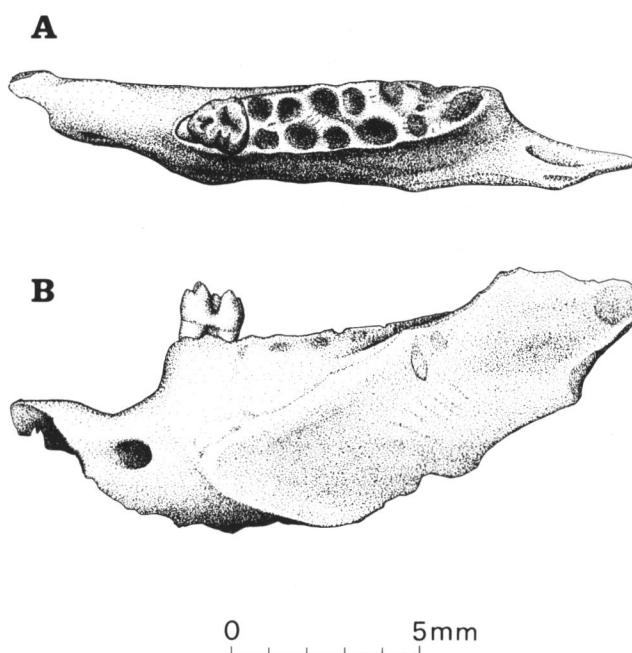


Fig. 95. *Pteromys momonga*. Left mandible with P_4 from Horizon I of Kannondo Cave Site (HUA-K00689). A, upper view; B, buccal view.

lower than the anterior cusp. The buccal wall of the crown is broadly grooved between the anterior cusp and hypoconid. The latter cusp is lower than the former, but higher than the mesoconid. The hypoconid is separated from the mesoconid by a narrow groove. The posterolophid connects the hypoconid with the entoconid, and forms the posterior wall of the crown. This loph is slender, and lower than the hypoconid and entoconid. The entoconid is the second largest cusp, and has the same height as the hypoconid. In occlusal view, it shows an elliptical shape elongated diagonally in HUA-K00330. In HUA-K00352, however, it is clearly divided into two cusps with the same size and height. The buccal one may be referred to hypoconulid.

The mesostylid is very small and much lower than the entoconid and anterior cusp in HUA-K00330. It is well separated from the last two cusps. In HUA-K00352, however, the mesostylid is absent. The talonid basin is shallow, and its floor is smoothed.

dP₄ has two thick roots. These roots have nearly the same size. Their cross sections are round. The anterior root extends antero-inferiorly, while the posterior one extends postero-inferiorly. The angle between the long axes of these roots is approximately 50° in HUA-K00330 and 45° in HUA-K00352.

*P*₄ —

The occlusal outline of the crown is broadly ovate. Four main cusps are situated on each corner of the crown, and surround the talonid basin. These cusps are usually conical. Of these, the metaconid is the highest. It is somewhat higher than the protoconid which has nearly the same height as the entoconid. The entoconid is slightly higher than the hypoconid.

The protoconid is well separated from the metaconid by a central longitudinal groove. This groove opens anteriorly between the paraconid and metaconid. The paraconid is attached on the middle of the anterior margin of the crown. Although this cusp is lower and much smaller than the protoconid, it is well defined and well separated from the protoconid and metaconid. In only one specimen (HUA-K00334) out of seven, however, it is quite indistinct. The paraconid is sometimes connected with the protoconid by a short ridge. In HUA-K00334, this ridge is swollen to be an additional small cusp attached on the buccal face of the paraconid. The metalophid is always lacking.

The mesoconid is much lower than the protoconid. It is triangular in occlusal view, and weakly connected with the protoconid and hypoconid by low and indistinct ridges. The hypoflexid is wide and deep. Its lingual part is divided into two parts by the mesoconid. The hypoconid is remotely isolated from the buccal end of the posterolophid. In five specimens out of seven, the entoconid is conical and differentiated from the posterolophid. In other two specimens (HUA-K00348 and 00350), however, it is well merged into this loph. The posterolophid is narrow, and gradually descends buccally. It is swollen to form a cusp near the entoconid in HUA-K00356. However such a cusp is not observed in other six specimens. The mesostylid is present in four specimens out of six, but absent from HUA-K00346 and 00356. If present, it is very small and indistinct.

The talonid basin is wide, and its floor is smoothed without a granulate enamel surface. This basin opens lingually between the metaconid and entoconid. From this opening, the

deepest part of the basin runs postero-buccally to reach the wide notch between the hypoconid and posterolophid.

P₄ is two-rooted. The cross section of the anterior root is round, while the posterior root has an elliptical cross section which is remarkably elongated transversely.

*M*₁ —

The outline of the crown is rhomboid. The lingual margin is not parallel to the buccal margin, so that the distance between them increases posteriorly. The basic structure of the crown is nearly identical with that of P₄. The following description is therefore focused on the characters different from those of P₄.

The protoconid is remotely separated from the metaconid. The former cusp is connected with the paraconid by a thick ridge. The buccal face of this ridge is always depressed just in front of the protoconid. The paraconid is better developed than in P₄. It is somewhat elongated transversely, and contacts with the metaconid. A strong cingulum is usually present on the anterior face of the metaconid. However it is weak in HUA-K00358, and absent from HUA-K00333. The metalophid extends lingually from the protoconid to reach the postero-buccal base of the metaconid. However this loph is weak and becomes indistinct lingually. A distinct closed groove is observed between the metalophid and paraconid. It is narrowly elliptic in occlusal view, and extends diagonally against the long axis of the crown.

The hypolophid is usually absent. However it is observed only in two specimens (HUA-K00333 and 00349) out of seven, where it extends lingually from the mesoconid as a short and weak ridge. The posterior face of the hypoconid is almost always smoothed, but a weak cingulum is observed there only in one specimen (HUA-K00333) out of seven.

A cusp is often recognized on the posterolophid near the entoconid. In three specimens (HUA-K00346, 00357 and ASM 700037) out of seven, however, it is absent. The mesostylid is present in five specimens out of eight. However it is small and weak, and attached on the posterior base of the metaconid. On the other hand, it is completely absent from other three specimens (HUA-K00326, 00346 and 00358).

M₁ has four roots. Their cross sections are round. Of these four, the postero-buccal one is generally the largest. It is slightly larger than or nearly as large as the antero-lingual root which is larger than or as large as the antero-buccal one. The postero-lingual one is generally the smallest.

*M*₂ —

The outline of the crown is rhomboid, but clearly different from that of M₁ in the following point: The lingual margin is parallel to the buccal margin as well as to the long axis of the crown. Therefore the width across the anterior part is nearly the same as that across the posterior part. The arrangement, relative size and height of each cusp and ridge are almost identical with those of M₁.

The buccal face of the ridge between the protoconid and paraconid is remarkably grooved. This groove is more distinct than in M₁. The metalophid is always present, but it is slender and weak. The cingulum on the anterior face of the metaconid is almost always present, but absent from only one specimen (HUA-K00328) out of nine. In case it is present, it is usually

well-developed. In two specimen (KUJC98066 and HUA-K00322), the buccal end of this cingulum is represented by one or two very small cusplets.

The hypolophid is usually absent. However it is present in three specimens (HUA-K00322, 00327 and 00331) out of nine. If present, this loph is very short and weak. Only in HUA-K00322, adding to this loph, a weak lingual projection is observed immediately anterior to the mesoconid. The posterior face of the hypoconid is weakly depressed in most specimens, but smoothed in only one specimen (HUA-K00347) out of nine. The posterolophid is clearly connected with the hypoconid at its buccal end, although the posterolophid there is somewhat lower than the other part of the same loph. Therefore the talonid basin does not open postero-buccally. The central part of the posterolophid is somewhat swollen, but does not become cusp-like in most specimens (seven specimens out of nine). In other two specimens (HUA-K00331 and 00337), one or two cusps are observed on this loph. The mesostylid is usually present (in seven specimens out of nine). If present, it is independent from the metaconid and entoconid (in three specimens), or attached on the postero-lingual base of the metaconid (in four specimens). The degree of its development is considerably variable.

M_2 almost always has four roots. In one specimen (HUA-K00338) out of seven, however, the postero-lingual and postero-buccal roots are fused to form a large root which is elongated transversely. This root is remarkably constricted centrally, which indicates the fusion of these two roots. In this case, the number of roots is three. In other five specimens, the postero-buccal root is the largest, and broadly elliptical in cross section. The antero-lingual, antero-buccal and postero-lingual roots have nearly the same size, and are round in cross section. In the remaining specimen (KUJC98066), the postero-buccal root is nearly the same size as the antero-lingual root which exceeds the antero-buccal root in size. Moreover the last root is as large as the postero-lingual root.

M_3 —

M_3 is represented by two specimens only (HUA-K00329 and 00345). The occlusal outline of the crown is obovate. The pattern of the anterior half of the crown is well coincident with those of M_1 and M_2 . However the posterior half is remarkably enlarged posteriorly in M_3 .

The paraconid is indistinct, and forms a part of the ridge which connects the protoconid with the metaconid. This ridge is more elongated than in M_1 and M_2 . The buccal face of this ridge immediately anterior to the protoconid is deeply grooved. The metalophid is weak and descends lingually. Its lingual end barely reaches the postero-buccal base of the metaconid. The closed valley in front of this ridge extends transversely. The cingulum on the anterior face of the metaconid is present in HUA-K00329, but absent from HUA-K00345. The hypoflexid is enlarged antero-posteriorly, and much wider than in M_1 . In HUA-K00329, a small additional tubercle is observed on the buccal opening of this valley just anterior to the hypoconid. It is low and indistinct. However this tubercle is lacking in HUA-K00345. The ectolophid between the protoconid and hypoconid is more distinct than in M_1 and M_2 .

The hypolophid branches off from the middle of the ectolophid between the mesoconid and hypoconid, and extends transversely to reach the entoconid. This ridge is weak and low in

HUA-K00345, but rather strong and high in HUA-K00329. In the latter specimen, an additional short lingual projection is observed on the ectolophid just anterior to the mesoconid. The buccal face of the posterolophid is grooved just behind the hypoconid. This groove is short, and opens postero-buccally. The posterolophid is thick, and connects the hypoconid with the entoconid. The mesostylid is absent. The talonid basin is divided into wider anterior part and much narrower posterior part by the hypolophid. The floor of this basin is smoothed.

The roots of M_3 are preserved in HUA-K00345 only. They are the antero-buccal root below the protoconid, antero-lingual root below the metaconid, posterior root below the posterior part of the talonid basin and hypolophid, and the middle lingual root below the entoconid. The posterior root is broadly elliptic in cross section. It is much larger than the other three roots. The antero-lingual root is slightly larger than the remaining two roots which have nearly the same size. These three roots have round cross sections.

Measurements

Only one specimen (HUA-K00689) is available for the present measurements of mandible. It is measured as follows (in mm):

Length of the cheek tooth row (P_4 to M_3) at the alveoli $8.07 \pm$

Length of the molar row (M_1 to M_3) at the alveoli..... 6.26

The measurements of the upper and lower cheek teeth are given in Tables 29 and 30 respectively. The latter measurements are also plotted in the scatter diagram of Fig. 96.

Comparison and Discussion

The present fossils can be assigned to a single species, because they generally have a uniform pattern and unimodal distribution of size in each tooth (Fig. 96). The two available

Table 29. Measurements of the upper cheek teeth of *Pteromys momonga* in mm. All the specimens are collected from the Late Pleistocene horizons of Kannondo Cave Site.

HORIZON AND SPECIMEN NUMBER	P^4		M^1		M^2		M^3	
	LENGTH	WIDTH	LENGTH	WIDTH	LENGTH	WIDTH	LENGTH	WIDTH
Upper part of Horizon M								
HUA-K00323	—	—	1.71	—	—	—	—	—
HUA-K00332	—	—	—	—	—	—	2.04	1.94
HUA-K00335	—	—	1.90	2.09	—	—	—	—
HUA-K00336	—	—	—	—	1.97	2.18	—	—
Horizon N								
HUA-K00341	—	—	1.75	2.10	—	—	—	—
HUA-K00343	—	—	1.71	2.00	—	—	—	—
HUA-K00344	1.77	1.84	—	—	—	—	—	—
Lower part of Horizon O								
HUA-K00354	—	—	1.63	1.78	—	—	—	—

Table 30. Measurements of the lower cheek teeth of *Pteromys momonga* in mm.

LOCALITY & SPECIMEN NUMBER	LENGTH	WIDTH	LOCALITY & SPECIMEN NUMBER	LENGTH	WIDTH
dP_4			M_2		
Kannondo Site (Late Pleist. horizons)			Kannondo Site (Late Pleist. horizons)		
HUA-K00330	1.27	0.85	HUA-K00322	2.28	2.11
HUA-K00352	1.33	0.98	HUA-K00327	2.21	1.97
P_4			HUA-K00328	2.29	2.09
Kannondo Site (Holocene horizons)			HUA-K00331	2.32	2.21
HUA-K00689	1.80	1.48	HUA-K00337	2.04	1.91
Kannondo Site (Late Pleist. horizons)			HUA-K00338	2.15	1.91
HUA-K00321	1.89	1.78	HUA-K00339	2.16	2.06
HUA-K00334	2.04	—	HUA-K00347	2.19	2.10
HUA-K00346	1.71±	1.76	Locality 3 of Ube Kosan Quarry		
HUA-K00348	1.66	1.43	KUJC98066	2.03	2.00
HUA-K00350	1.72	—	M_3		
HUA-K00356	1.62	1.32	Kannondo Site (Late Pleist. horizons)		
M_1			HUA-K00329	2.81	2.20
Kannondo Site (Late Pleist. horizons)			HUA-K00345	2.58	1.89
HUA-K00325	1.92	1.81			
HUA-K00326	2.01	1.86			
HUA-K00333	1.98	1.84			
HUA-K00342	1.94	—			
HUA-K00346	2.03	1.80			
HUA-K00349	1.83	1.65			
HUA-K00357	1.76	1.53			
HUA-K00358	1.76	1.75			

M_3 from the Late Pleistocene horizons of Kannondo Cave Site are considerably different from each other in size. However such a difference can be interpreted as two extremities in a single population, because the other kinds of cheek teeth from the same locality resemble these teeth in the degree of size variation. Moreover such size variation seems to be found in the recent population of *P. momonga*.

P. momonga is generally regarded as an independent species, which is now restricted to Honshu, Shikoku and Kyushu. In comparison with the living *P. momonga*, the present fossils are well coincident with it in tooth pattern and size. Therefore they can be assigned to *P. momonga*.

The closely related species, *P. volans*, is restricted to Hokkaido in the present Japanese Islands. However this species is widely distributed in the northern part of the Eurasian Continent from Europe to Eastern Siberia including North China and Korea. The differential characters between *P. volans* and *P. momonga* were given by CORBET (1978), but these concern skull instead of tooth. Unfortunately, the morphological data on the cheek teeth of *P. volans* are inadequately available for the present study. The available data are only represented by the illustration and description of the cheek teeth in MILLER (1912), and by their measurements in SULKAVA (1978). The materials which these authors used are obtained from Europe.

In comparison with MILLER's illustration (Fig. 196), the outlines of P^4 and M^3 are more triangular in the present fossils. In M^1 and M^2 of *P. volans*, a strong projection extends buccally from the endoloph into the paraflexus, while such a projection is absent or very weak

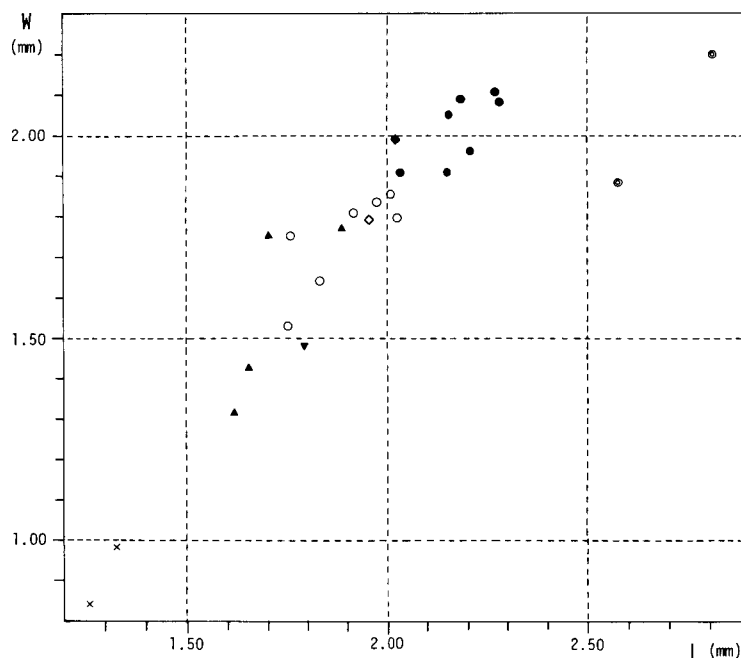


Fig. 96. Scatter diagram showing the relationship between the length and width of the cheek teeth of *Pteromys momonga*. Materials from the Late Pleistocene horizons of Kannondo Cave Site ($\times$ dP₄; $\blacktriangle$ P₄; $\circ$ M₁; $\bullet$ M₂; $\odot$ M₃); $\blacktriangledown$ P₄ from the Holocene horizons of Kannondo Cave Site; $\diamond$ M₁ from Tanuki-ana Cave; $\blacklozenge$ M₂ from Locality 3 of Ube Kosan Quarry.

in the corresponding teeth of the present fossils. The posterior cross loph of M³ is absent in *P. volans*, while it is clearly present in the present fossils. As regards SULKAVA's data, *P. volans* is obviously smaller than the present fossils. Therefore the present fossils are possibly distinguishable from *P. volans* of Europe. Because the intraspecific variation of the cheek teeth of this species is unknown, the direct comparison with *P. volans* of East Asia is necessary for the further study of the present fossils.

In 1976, KOWALSKI and HASEGAWA described dP⁴ and M₃ of *Pteromys* from the Middle Pleistocene sediments of Ando Quarry, and assigned them to *P. cf. volans*. The reason for this identification is the smaller size of M₃ which is well coincident with the measurements of only one specimen of the living *P. volans* from Hokkaido. However this M₃ is very near to the smaller variant of the present fossils in size. Therefore the teeth from Ando Quarry seem to be included in the same population as the present fossils. Because any significant reason for the identification as *P. cf. volans* can not be found, the present author prefers to treat the specimens from Ando Quarry as conspecific with *P. momonga*.

P. momonga was possibly originated from *P. volans* or its ancestral form. *P. volans* is an inhabitant of coniferous forests in the frigid or cold temperate zones of the Eurasian Continent. *P. volans* or its ancestor possibly immigrated from the continent into Honshu, Shikoku and Kyushu in the cold phase of Pleistocene. The adaptation to the temperate forests in these

areas seems to be the main cause of the speciation of *P. momonga* from its ancestor. Although KOWALSKI and HASEGAWA pointed out the possibility that *P. momonga* and *P. volans* were not differentiated in the period of the sediments of Ando Quarry, it can be inferred that the time of the speciation of *P. momonga* is still earlier.

Family Arvicolidae GRAY, 1821

Key to the genera of the Japanese arvicolids

Four arvicolid genera such as *Myopus*, *Clethrionomys*, *Phaulomys* and *Microtus* are known from Japan. Of these, *Myopus* is recorded only from the Middle Pleistocene sediments of Ikumo Quarry, but it is not available for the present study (for its description, see KOWALSKI and HASEGAWA, 1976). The key to these genera based on the osteological and dental characters is given below.

1. Larger; upper molar rows remarkably diversing posteriorly; lower incisor short, terminating at or slightly behind posterior end of M_2 , and wholly situated lingual to lower molars; enamel bands interrupting at tips of triangles; in M^1 and M^2 , buccal re-entrant angles much deeper than lingual ones, so that buccal triangles are remarkably larger than lingual ones; BRA1 of M^2 almost reaching lingual border of crown. M^3 comprising four transverse dentine fields; T2 elongating transversely; BRA1 and LRA3 very deep, which almost reach lingual and buccal borders of crown respectively. M_1 with only three triangles between anterior and posterior loops; in M_2 , T4 oval and separated from T3. M_3 broader and comprising three or four dentine fields which elongate transversely; BRA2 always absent; LRA1 and LRA2 very deep and almost reaching buccal border of crown. ***Myopus***
- Smaller; upper molar rows nearly parallel or slightly diversing posteriorly; lower incisor longer, passing from lingual to buccal sides between M_2 and M_3 , and extending far behind M_3 ; enamel bands generally continuous at tips of triangles; in M^1 and M^2 , buccal re-entrant angles almost as deep as lingual ones, so that size differences between lingual and buccal triangles are not so remarkable as in *Myopus*; BRA1 of M^2 reaching only central part of crown. M^3 comprising an anterior loop, three triangles and a posterior loop; T2 smaller and triangular; BRA1 and LRA3 much shallower than in *Myopus*. M_1 with more than three triangles between anterior and posterior loops; in M_2 , T4 more triangular, and separated from or confluent with T3. M_3 narrower, and always comprising three dentine fields; these fields not elongating transversely; BRA2 always present; LRA1 and LRA2 shallower. 2
2. Bony palate terminating posteriorly in complicate double shelved structure, where a remarkable median septum is present; area between ascending ramus and alveoli of lower molars deeply pocketed; capsule for lower incisor longer and more conspicuous on lingual face of ascending ramus; posterior end of lower incisor forming a tubercle on buccal face of condylar process; mandibular foramen situated more anteriorly, and much higher than occlusal surfaces of lower molars. Molars are rootless; thickness of enamel bands well differentiated from part to part; salient angles sharply pointed, so that triangles give more triangular appearance; triangles well alternating and closed. Second minor fold and second secondary fold of M^1 and M^2 (see Fig. 98) better developed and usually filled with cementum; anterior loop of M_1 variable in shape, which is generally larger and more complicate; Is 2 and Is 4 of M_2 always closed; first secondary fold and anterior labial fold of M_2 and M_3 (see Fig. 98) better developed and usually filled with cementum. ***Microtus***
- Posterior part of bony palate simpler; its posterior border straight without the median septum seen in *Microtus*; area between ascending ramus and alveoli of lower molars flattened or slightly concave; capsule for lower incisor shorter and inconspicuous on lingual face of ascending ramus; the tubercle on buccal face of condylar process lacking; mandibular foramen situated more posteriorly and approaching posterior border of ascending ramus; level of this foramen nearly as high as or only slightly higher than occlusal surfaces of lower molars. Molars rooted or unrooted; differentiation in thickness of enamel bands not so remarkable as in *Microtus*; salient angles generally blunter, so that triangles give somewhat

- rounded appearance; triangles alternating or sometimes opposing; second minor fold and second secondary fold of M^1 and M^2 less developed, where cementum is usually lacking; anterior loop of M_1 generally elliptical, which is generally smaller and simpler than in *Microtus*; in M_2 , Is 2 usually open, while Is 4 almost always open; first secondary fold and anterior labial fold of M_2 and M_3 less developed, where cementum is usually lacking. 3 ("***Clethrionomys-Phaulomys* group**")
3. Molars becoming rooted in life; salient angles somewhat more pointed; isthmuses tending to be closed (especially in M_1 , Is 2 and Is 4 closed or narrow). ***Clethrionomys***
- Molars remaining unrooted in life; salient angles somewhat blunter; isthmuses tending to be open (especially in M_1 , Is 2 and Is 4 usually broadly open). ***Phaulomys***

As regards "*Clethrionomys-Phaulomys* group," the boundary between these two genera can not be clearly defined, when the fossil materials from some Late Pleistocene localities are taken into consideration. In order to describe these fossil materials, the concept of an intermediate form between these two genera is introduced here. In such an intermediate form, the time of root-formation is very late in life, so that the molars with roots or with sign of root-formation are rarely found in the fossil assemblages. This intermediate form is called "*Clethrionomys-Phaulomys* transitional form" here. The part of "*Clethrionomys-Phaulomys* group" in the key described above can be modified for the convenience of the classification of fossil materials, when "*Clethrionomys-Phaulomys* transitional form" is added.

***Clethrionomys-Phaulomys* group**

3. Molars with roots or sign of root-formation frequently found in a single fossil assemblage (generally more than 40% of total specimens). ***Clethrionomys***
- Molars with roots or sign of root-formation rarely found in a single fossil assemblage (less than 5%). ***Clethrionomys-Phaulomys* transitional form**
- All molars in a single fossil assemblage not showing any sign of root-formation. ***Phaulomys***

Genus *Clethrionomys* TILESIIUS, 1850

Characters

The following common characters are observed in the Japanese fossil and living species of *Clethrionomys*:

The interorbital region is broad and flattened. The bony palate terminates posteriorly in simple structure rather than in *Microtus* (Fig. 102 and 137). The depression between the alveoli of the lower molars and the ascending ramus is inconspicuous. The capsule for the lower incisor on the lingual face of the ascending ramus is much weaker than in *Microtus*. The posterior end of the lower incisor is nearly as high as the level of the occlusal surfaces of the lower molars.

The molars are rooted at least in grown stage of life. The number of roots is two in all kinds of the molars. The salient angles are generally more acutely pointed than in *Phaulomys*, but somewhat blunter than in *Microtus*. The re-entrant folds are filled with rich cementum. The enamel band thins off at the bottom of each re-entrant fold. In each triangle, the enamel on the concave side is generally as thick as that on the convex side. M^1 and M^2 are normal in pattern, and always lack an additional postero-lingual angle. T1 and T3 of M^1 and T3 of M^2 are not so elongated obliquely as in *Microtus*. M^3 is subject to a wide range of variation in the complexity of the posterior loop. The anterior loop of M_1 is generally small and elliptical in

shape. BSA3 of M_3 is always well-developed.

Age-class of molars

In young individuals of *Clethrionomys*, the basal parts of the re-entrant folds and the pulp-cavities are completely open. As the individuals grow up, these parts are gradually closed to form roots. The following morphological changes are observed in sequence during the root-formation:

1. The basal parts of the re-entrant folds start to close. Four stages such as "open," "half-closed," "just-closed" and "closed" are morphologically distinguishable during the closing process of these parts as show in Fig. 97.
2. After the closing of the basal parts of the re-entrant folds, the neck is formed, so that the incipient root is separated from the crown.
3. The pulp-cavity is constricted at the central part with the growth of the incipient root.
4. As the root still lengthens, it is divided into anterior and posterior parts.
5. Each root gradually increases in length. On the contrary, the height of the crown diminishes.

On the basis of these morphological changes, the isolated molars of this genus can be classified into several age-classes. ABE (1973) provided a criterion for the classification of the age-classes in his study of the living *Clethrionomys* of Hokkaido. Unfortunately his criterion is concerned to M^2 only. Therefore new criteria applicable to all kinds of the molars are proposed in the present paper. Such criteria are coincident with ABE's one in four age-classes (I, IV, V and VI), but include some modifications in other age-classes (II and III). Moreover the age-class Y is newly introduced. The age-classes defined by these new criteria are described as follows (Figs. 103–105, 107–109):

Age-class Y: The youngest age-class. The specimens belonging to this age-class is considerably smaller than others, and have unique characters in occlusal pattern which are indicative of the incipient stage of wear. They are: (1) salient angles sharply pointed; (2) ithmuses broadly open; (3) enamel thin; (4) cementum absent or poor in re-entrant folds. These characters are never observed in the specimens older than the age-class Y. The basal parts of the re-entrant folds are broadly open.

Age-class I: The specimens of this age-class are larger than those of the age-class Y. The former is easily distinguished from the latter by the lack of the characters in occlusal pattern of the age-class Y. However the basal parts of the re-entrant folds of the former are broadly open as those of the latter.

Age-class II: This age-class is generally defined by the "half-closed" condition of the basal parts of the re-entrant folds. However each re-entrant fold does not always become "half-closed" simultaneously. Moreover the manner of the closing is considerably variable by tooth kind. Therefore this age-class is defined by different criteria in each molar.

M^1 (Fig. 103) — The basal parts of LRA2 and BRA1 are always "half-closed," while those

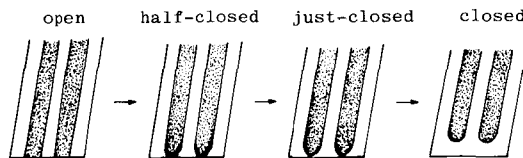


Fig. 97. Diagrammatic representation for the process of closing of the basal parts of the re-entrant folds. Four stages are recognized; namely "open," "half-closed," "just-closed" and "closed."

of LRA1 and BRA2 are usually "half-closed."

M² (Fig. 104) — The basal part of LRA2 is always "half-closed," while those of BRA1 and BRA2 are usually "half-closed."

M³ (Fig. 105) — The basal part of LRA4 is already "closed," while that of BRA3 is "half-closed" or "just-closed." Others are still "open."

M₁ (Fig. 107) — The basal part of LRA4 is already "closed," while that of BRA3 is "half-closed." Others are still "open."

M₂ (Fig. 108) — The basal parts of LRA2, BRA1 and BRA2 are "half-closed." That of LRA1 is "open" or "half-closed."

M₃ (Fig. 109) — The basal part of BRA2 is "just-closed" or "closed," while that of BRA1 is "open" or "just-closed." Those of LRA1 and LRA2 are usually "open."

Age-class III: This age-class is generally defined by the "just-closed" condition of the basal parts of the re-entrant folds. By the same reason as in the age-class II, the criteria of this age-class are given independently in each molar.

M¹ (Fig. 103) — The basal parts of all the re-entrant folds are "just-closed."

M² (Fig. 104) — The basal parts of BRA1 and BRA2 are "just-closed," while that of LRA2 is "closed."

M³ (Fig. 105) — The basal parts of LRA4 and BRA3 are "closed." Those of LRA2 and LRA3 are "just-closed" or "half-closed," while those of BRA1 and BRA2 vary from "just-closed" to "open."

M₁ (Fig. 107) — The basal parts of LRA4 and BRA3 are already "closed." Those of LRA2, LRA3 and BRA2 are "just-closed" or "half-closed," while that of LRA1 varies from "just-closed" to "open."

M₂ (Fig. 108) — The basal parts of LRA1, LRA2 and BRA2 are "just-closed," while that of BRA1 is "just-closed" or "closed."

M₃ (Fig. 109) — The basal parts of BRA1 and BRA2 are "closed," while that of LRA2 is "half-closed" or "just-closed." That of LRA1 is "half-closed" or "open."

Age-class IV: The basal parts of all the re-entrant folds are completely "closed." The pulp-cavity is slightly constricted at the central part.

Age-class V: The basal parts of all the re-entrant folds are completely "closed." The pulp-cavity is strongly constricted at the central part.

Age-class VI: The oldest age-class. The anterior and posterior roots are formed by the division of the incipient root.

Because the ontogenetic change is practically gradual, the specimens with intermediate characters between two neighbouring age-classes are sometimes found. These specimens are assigned to an intermediate age-class written in a hyphenated name of two neighboring age-classes (for example, VI-V, III-II etc.).

It should be noted that the time of the root-formation varies with tooth kind. Therefore these age-classes indicate only relative ages of each molar. For instance, the age-class III of M₁ is not always as old as the same age-class of M₂ in the strict sense.

Method of morphological analysis of molars

In his revision of the classification of the Japanese living red-backed voles (*Clethrionomys* and *Phaulomys* in the present paper), AIMI (1980) closely analysed the variation in molar patterns as well as in skull characters. In order to compare with his numerous data, the same dental characters as he examined are also observed in the present study. They are: (1) closing or opening of each isthmus; (2) minute characters other than the isthmuses.

As regards (1), AIMI offered a criterion whether an isthmus is close or open. He defined

the isthmus as "closed," when its minimum width measured between the outer surfaces of both lingual and buccal enamel bands is less than 0.1 mm. Although the isthmus widths of molars are measured between the inner surfaces of both lingual and buccal enamel bands in *Microtus* (p. 276, Fig. 125), AIMI's criterion is employed not only in this section but also in the sections of *Phaulomys* and *Clethrionomys-Phaulomys* transitional form. When the frequency of closing of each isthmus is calculated as the specific character, the specimens of the age-class Y are excluded from the analysed populations.

As regards (2), the following features are observed (Fig. 98):

Upper Molars

1. Shape of the anterior wall of the anterior loop (whether single-lobed, bilobed or trilobed).
2. Relative size of the lingual and buccal parts of the anterior loop of M^1 . These parts are called anterolingual conule and anterolabial conule by AIMI.
3. Concavity of the postero-lingual wall of T3 and the lingual wall of T4 observed on the occlusal surfaces of M^1 and M^2 (degree of development of the second minor fold by AIMI).
4. Concavity of the postero-buccal wall of T4 observed on the occlusal surfaces of M^1 and M^2 (degree of development of the second secondary fold by AIMI).

Lower Molars

5. Shape of the anterior wall of the anterior loop of M_1 (whether single-lobed, bilobed or trilobed).
6. Relative size of the lingual and buccal parts of the anterior loop of M_1 . These parts are called anterolingual conulid and anterolabial conulid by AIMI.
7. Concavity of the antero-lingual wall of T3 and the lingual wall of T4 observed on the occlusal surfaces of M_2 and M_3 (degree of development of the first secondary fold by AIMI).
8. Concavity of the antero-buccal wall of T4 observed on the occlusal surfaces of M_2 and M_3 (degree of development of the anterior labial fold by AIMI).
9. Shape of the posterior wall of the posterior loop (whether single-lobed or bilobed in M_1 and M_2 ;

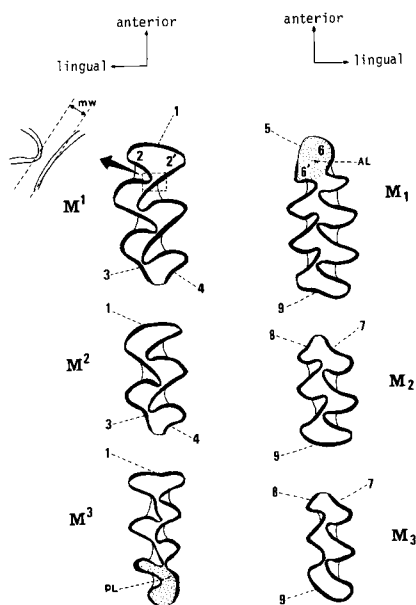


Fig. 98. Method of measurements of the minimum width of each isthmus (mw), and characters of the molars observed in the present paper (1 to 9, PL and AL). These method and observations are applied not only to *Clethrionomys* but also to *Phaulomys* and *Clethrionomys-Phaulomys* transitional form.

1, anterior wall of anterior loop; 2, lingual part of anterior loop of M^1 (anterolingual conule); 2', buccal part of anterior loop of M^1 (anterolabial conule); 3, postero-lingual wall of T3 and lingual wall of T4 (second minor fold); 4, postero-buccal wall of T4 (second secondary fold); 5, anterior wall of anterior loop of M_1 ; 6, lingual part of anterior loop of M_1 (anterolingual conulid); 6', buccal part of anterior loop of M_1 (anterolabial conulid); 7, antero-lingual wall of T3 and lingual wall of T4 (first secondary fold); 8, antero-buccal wall of T4 (anterior labial fold); 9, posterior wall of posterior loop; PL, posterior loop of M^3 ; AL, anterior loop of M_1 .

and degree of development of the second minor fold and posteroconulid in M_3 by A_{IM1} .

The shape of the posterior loop of M^3 generally has great importance for the classification of arvicolids. MRYAO (1967) provided eight morphotypes to analyse the morphological variation of this part of the living arvicolids of Honshu (his Fig. 2). Subsequently ABE (1973) illustrated the variation in M^3 of the living *Clethrionomys* of Hokkaido, and recognized 12 morphotypes (his Fig. 4). In the present paper, the following eight morphotypes are newly proposed (Fig. 99):

1. Normal type with broadly open Is 6.

Morphotype S: Simplest type; posterior loop very simple where LRA4, LSA5 and BSA4 are never recognized.

Morphotype L₁: Posterior loop upside-down L-shaped, so that LRA4 is weakly developed. BSA4 is absent.

Morphotype L₂: Posterior loop with the same feature as the morphotype L_1 except the presence of BSA4.

Morphotype C₁: Posterior loop C-shaped, so that LRA4 and LSA5 are well developed. BSA4 is absent.

Morphotype C₂: Posterior loop with the same feature as the morphotype C_1 except the presence of BSA4.

Morphotype F₁: Posterior loop F-shaped, so that LRA4 and LSA5 are well developed, and LRA5 is recognized. However BSA4 is absent.

Morphotype F₂: Posterior loop with the same feature as the morphotype F_1 except the presence of BSA4.

2. Abnormal type. Is 6 is narrow or "closed," so that the posterior loop is divided into anterior and posterior parts.

Morphotype Ab: LRA4 and LSA5 are well developed. Moreover BSA4 is present.

The relationship among these morphotypes and those of the other authors is given in Table 31.

31. The morphotypes of the present paper are applicable not only to *Clethrionomys* but also to *Phaulomys* and *Clethrionomys-Phaulomys* transitional form.

The morphology of the anterior loop of M_1 is also important for the classification of arvicolids. In *Clethrionomys* as well as in *Phaulomys* and *Clethrionomys-Phaulomys* transitional form, the variation of this part depends mainly on the width of Is 6 and the depth of LRA4. The following four morphotypes are recognized on the basis of these characters (Fig. 100):

Morphotype 1: LRA4 is well-developed, and Is 6 is closed or narrow, so that the anterior loop is adequately independent from T5.

Morphotype 2: LRA4 is well-developed, but Is 6 is broader than that of the morphotype 1.

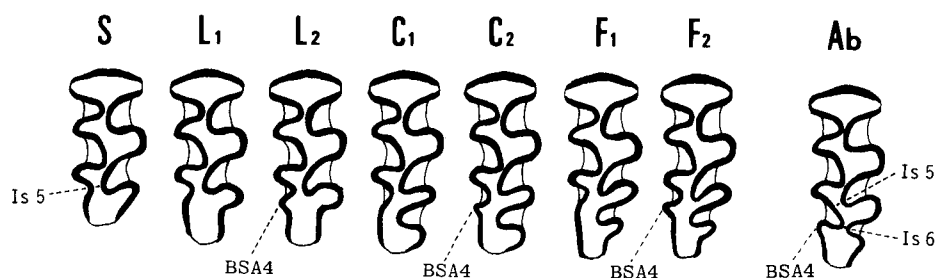
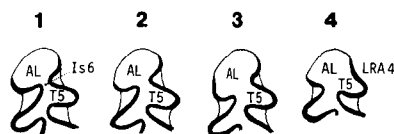


Fig. 99. Morphotypes of M^3 for *Clethrionomys*, *Clethrionomys-Phaulomys* transitional form and *Phaulomys*. For detailed explanation of each morphotype see text.

Table 31. Relationship among the morphotypes of M^3 by the present author, by MIYAO (1967) and by ABE (1973).

Morphotypes of the present paper	Miyao's Morphotypes	Abe's Morphotypes
S	I (simplest type)	7, 8, 9, 10
L ₁	II	6
L ₂	III	6'
C ₁	IV	4, 5
C ₂	V	2, 3, 4'
F ₁	VI	None
F ₂	VII	1
Ab	None	None

Fig. 100. Morphotypes of M_1 for *Clethrionomys*. For detailed explanation see text. These morphotypes are also applicable to *Phaulomys* and *Clethrionomys-Phaulomys* transitional form.

Morphotype 3: LRA4 is moderately developed, and Is 6 is broadly open.

Morphotype 4: LRA4 is weak or faint, and Is 6 is very broad, so that the anterior loop is well confluent with TS.

Remarks on the fossil *Clethrionomys* in East Asia

The fossils of *Clethrionomys* are extremely rare in China. They have been reported from only three localities as far as the available references are concerned (Fig. 101; Table 32). From Locality 1 of Choukoutien, YOUNG (1934) recorded only two mandibles of *C. rufocanus* within thousands of the arvicolid remains. *Clethrionomys* is also rare in the arvicolid assemblage of Ku-hsiang-tung. Although TOKUDA (1939) identified two mandibles as a single species, *C. rufocanus*, they are considerably different in size and pattern from each other. Judging from his illustration (Text-fig. 3), larger and smaller ones are possibly assignable to *C. rufocanus* and *C. rutilus* (or its allied form) respectively.

The fossils of *Clethrionomys* are known from the Quaternary sediments of several fossil localities in Transbaikalia and Eastern Siberia (VANGENGIM, 1961; ERBAJEVA, 1970; AGADJANIAN and ERBAJEVA, 1983). They are referred to *C. rufocanus*, *C. rutilus* or *C. sp.* Their occurrences are, however, rare in the micro-mammalian assemblages of these localities.

In contrast to the circumstances in the continent, *Clethrionomys* is a predominant element in the arvicolid fauna of the Japanese Middle Pleistocene. The fossils are recorded from five

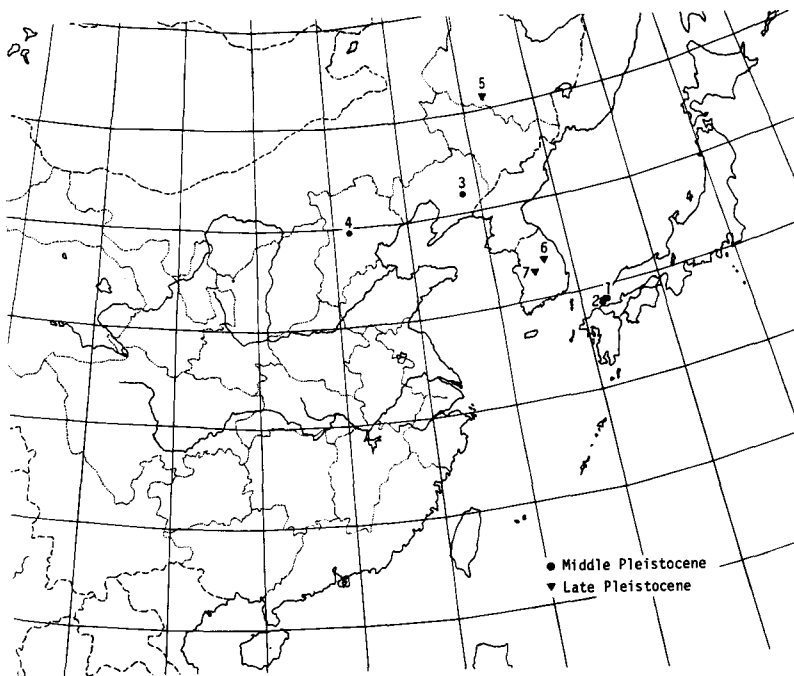


Fig. 101. Middle and Late Pleistocene fossil localities of *Clethrionomys* in East Asia. 1, Ikumo Quarry; 2, Akiyoshi Area (including Ando Quarry and Localities 1, 3 and 4 of Ube Kosan Quarry); 3, Miaohoushan; 4, Locality 1 of Choukoutien; 5, Ku-hsiang-tung; 6, Chommal Yonggul Cave; 7, Turubong Cave. For detailed explanation see Table 32.

localities, and are exclusively assigned to *C. japonicus* (Fig. 101; Table 32). It is inferred that this species was evolved to be *Phaulomys* in Japan during the Late Pleistocene as discussed in the subsequent sections. Although the rooted arvicolid molars sometimes obtained from the Late Pleistocene localities of Honshu were previously assigned to *Clethrionomys*, they are included in "*Clethrionomys-Phaulomys* transitional form" in the present paper (p. 240).

Key to the species of the Japanese *Clethrionomys*

1. Size larger; postero-lateral bridge of palatine present; alveolus of M_3 forming a protuberant area on lingual face of horizontal ramus; time of root-formation later in life; salient angles somewhat blunter, so that triangles are slightly rounded; isthmuses of upper molars usually or always closed; M^1 longer than M^3 ; second minor fold and second secondary fold of M^1 and M^2 more or less developed. In M^3 , anterior loop transversely narrowly elliptical; BRA1 shallower than BRA2; posterior loop variable, but generally simpler. Anterior loop of M^1 elliptical, and its buccal part not remarkably elongating postero-buccally; M_2 and M_3 relatively narrower; first secondary fold and anterior labial fold of these molars more or less developed. 2
- Size smaller; postero-lateral bridge of palatine absent; alveolus of M_3 not forming a protuberant area on lingual face of horizontal ramus; time of root-formation earlier in life; salient angles acutely pointed, and triangles regularly triangular; isthmuses of upper molars tending to be uniformly open; M^1

Table 32. Pleistocene fossil localities of *Clethrionomys* in East Asia. The numbers on the left side correspond to those in Fig. 101.

LOCALITY	IDENTIFICATION (PARTLY REVISED)	REFERENCES	REMARKS
MIDDLE PLEISTOCENE			
1. Ikumo Quarry	<i>Clethrionomys japonicus</i>	Hasegawa (1963, 1966); Kowalski & Hasegawa (1976); this paper	Previously assigned to <i>Clethrionomys</i> sp. or <i>C.</i> <i>rufocanus</i> .
2. Ando Quarry	<i>Clethrionomys japonicus</i>	Hasegawa (1966, 1972); Kowalski & Hasegawa (1976); Hasegawa et al. (1977); this paper	Previously assigned to <i>Clethrionomys rufocanus</i> <i>andersoni</i> , C. sp. or <i>C.</i> <i>rufocanus</i> .
2. Locality 3 of Ube Kosan Quarry	<i>Clethrionomys japonicus</i>	This paper	
2. Locality 1 of Ube Kosan Quarry	<i>Clethrionomys japonicus</i>	This paper	
2. Locality 4 of Ube Kosan Quarry	<i>Clethrionomys japonicus</i>	This paper	
3. Miaohoushan	<i>Clethrionomys rufocanus</i>	Zhang (1981); Zhang et al. (1986)	
4. Locality 1 of Chou- koutien	<i>Clethrionomys rufocanus</i>	Young (1934); Kahlke & Chow (1961)	
LATE PLEISTOCENE			
5. Ku-hsiang-tung	<i>Clethrionomys rufocanus</i> ? <i>Clethrionomys rutilus</i>	Tokuda (1939); Tokunaga & Naora (1939)	Tokuda originally assigned them to <i>Clethrionomys</i> <i>rufocanus</i> .
6. Chommal Yonggul Cave	<i>Clethrionomys rufocanus</i> <i>Clethrionomys</i> sp.	Sohn (1984)	No descriptions are given.
7. Turubong Cave	<i>Clethrionomys</i> sp.	Sohn (1984)	Ditto.

generally shorter than M^3 ; second minor fold and second secondary fold of M^1 and M^2 always undeveloped. In M^3 , anterior loop more rectangular; BRA1 nearly as deep as BRA2; posterior loop more complicate. Buccal part of anterior loop of M_1 remarkably elongating postero-buccally; M_2 and M_3 relatively broader; first secondary fold and anterior labial fold of M_2 and M_3 always undeveloped.

- *C. rutilus*
2. Size larger; second secondary fold of M^1 and M^2 better developed; posterior loop of M^3 simple; three salient angles generally present on lingual side of M^3 ; LRA4 of M_1 usually deeper; Is 2 and Is 5 of M_1 usually closed; first secondary fold of M_2 and M_3 , and anterior labial fold of M_3 better developed. *C. rufocanus*
- Size smaller (intermediate between *C. rufocanus* and *C. rutilus*); second secondary fold of M^1 and M^2 less developed; posterior loop of M^3 simple or complicate; three or four salient angles present on lingual side of M^3 ; LRA4 of M_1 more frequently shallow; Is 2 and Is 5 of M_1 usually open, but the former relatively narrow; first secondary fold of M_2 and M_3 , and anterior labial fold of M_3 less developed. *C. japonicus*, sp. nov.

***Clethrionomys japonicus*, sp. nov.**

(Figs. 102–109; Pls. 1–15)

Synonym —

Clethrionomys rufocanus SUNDEVALL; KOWALSKI and HASEGAWA 1976 (in part), *Bull. Nat. Sci. Mus. Ser. C.*, **2**,

48–52; from Sumitomo Quarry, Ikumo Quarry and Ando Quarry.
Clethrionomys sp.; HASEGAWA *et al.* 1977, *Quat. Res. (Daiyonki-kenkyu)*, **16**, 15–16; from Ando Quarry.

Holotype — Skull fragment with right M¹, M² and M³ from Locality 3 of Ube Kosan Quarry (KUJC96390).

Paratypes — Left mandible with I, M₁, M₂ and M₃ from Layer 4 of Ube Kosan Quarry (KUJC96324); left mandible with I, M₁ and M₂ from the same horizon and locality (ASM 700002).

Referred materials —

Ikumo Quarry

1 isolated M³ (ASM 700006); 1 isolated M₁ (ASM 700003); 2 isolated M₂ (ASM 700004, 700007); 2 isolated M₃ (ASM 700005, 700008).

Locality 4 of Ube Kosan Quarry

6 isolated M¹ (ASM 700039 a–f); 4 isolated M² (ASM 700040 a–d); 1 isolated M₁ (ASM 700041); 3 isolated M₂ (ASM 700042 a–c); 6 isolated M₃ (ASM 700043 a–f).

Locality 3 of Ube Kosan Quarry

Layer 1: 2 maxillae with M¹ (KUJC96520, 96521); 19 isolated M¹ (KUJC96505–96519, 96522–96525); 22 isolated M² (KUJC96628–96649); 26 isolated M³ (KUJC96388, 96389, 96391–96407, 96992–96998); 3 mandibles with I, M₁ and M₂ (KUJC96275, 96295, 96296); 2 mandibles with M₁ and M₂ (KUJC96280, 96282); 1 mandible with M₁ (KUJC96276); 1 mandible with M₂ (KUJC96281); 1 mandible with I (KUJC96990); 2 mandibles without teeth (KUJC96989, 96991); 18 isolated M₁ (KUJC96277–96279, 96283–96294, 96297, 96298, 96504); 19 isolated M₂ (KUJC96753–96770, 96999); 24 isolated M₃ (KUJC96865–96888).

Layer 2: 14 isolated M¹ (KUJC96526–96538, 97002); 12 isolated M² (KUJC96650–96661); 17 isolated M³ (KUJC96408–96424); 3 mandibles with I, M₁ and M₂ (KUJC96302, 96307, 96308); 2 mandibles with M₁ and M₂ (KUJC96299, 96300); 1 mandible with M₂ (KUJC96303); 2 mandibles without teeth (KUJC97003, 97004); 7 isolated M₁ (KUJC96301, 96304–96306, 96309, 96310, 97001); 11 isolated M₂ (KUJC96771–96781, 97000); 21 isolated M₃ (KUJC96889–96909).

Layer 3: 1 maxilla with M¹ (KUJC96544); 11 isolated M¹ (KUJC96539–96543, 96545–96548, 97006, 97008); 8 isolated M² (KUJC96662–96668, 97007); 10 isolated M³ (KUJC96425–96434); 3 mandibles with I, M₁ and M₂ (KUJC96311–96313); 1 mandible with M₁ and M₂ (KUJC96314); 1 mandible with M₂ (KUJC96315); 1 mandible without teeth (KUJC97005) 8 isolated M₁ (KUJC96316–96323); 6 isolated M₂ (KUJC96782–96787); 13 isolated M₃ (KUJC96910–96922).

Layer 4: 2 maxillae with M¹ (KUJC96549, 96560); 10 isolated M¹ (KUJC96550–96559); 12 isolated M² (KUJC96669–96680); 8 isolated M³ (KUJC96435–96442); 4 mandibles with I, M₁, M₂ and M₃ (KUJC96325, 96327, 96328, 96330); 1 mandible with M₁, M₂ and M₃ (KUJC96326); 1 mandible with I, M₁ and M₂ (KUJC96329); 1 mandible with M₁ and M₂ (KUJC96331); 4 isolated M₁ (KUJC96332–96335); 11 isolated M₂ (KUJC96788–96798); 10 isolated M₃ (KUJC96923–96932).

Layer 5: 3 isolated M¹ (KUJC96601–96603); 2 isolated M² (KUJC96720, 96721); 3 isolated M₁ (KUJC96364–96366); 2 isolated M₂ (KUJC96838, 96839); 1 isolated M₃ (KUJC96967).

Layer 6: 4 isolated M¹ (KUJC96621–96624); 12 isolated M² (KUJC96740–96751); 3 isolated M³ (KUJC96497, 96498, 97023); 1 mandible without teeth (KUJC97022); 7 isolated M₁ (KUJC96381–96387); 6 isolated M₂ (KUJC96859–96864); 5 isolated M₃ (KUJC96981–96985).

Layer 8: 12 isolated M¹ (KUJC96589–96600); 10 isolated M² (KUJC96712–96719, 97014, 97015); 17 isolated M³ (KUJC96473–96488, 97013); 1 mandible with I, M₁ and M₂ (KUJC96354); 10 isolated M₁ (KUJC96355–96363, 97012); 10 isolated M₂ (KUJC96828–96837); 11 isolated M₃ (KUJC96956–96966).

Layer 9: 9 isolated M¹ (KUJC96580–96588); 10 isolated M² (KUJC96702–96711); 6 isolated M³ (KUJC96467–96472); 1 mandible without teeth (KUJC97011); 5 isolated M₁ (KUJC96349–96353); 11 isolated M₂ (KUJC96817–96827); 8 isolated M₃ (KUJC96948–96955).

Layer 10: 5 isolated M¹ (KUJC96575–96579); 9 isolated M² (KUJC96693–96701); 10 isolated M³ (KUJC96458–96466, 97010); 5 isolated M₁ (KUJC96344–96348); 10 isolated M₂ (KUJC96807–96816); 7 isolated M₃ (KUJC96941–96947).

- Layer 11: 2 isolated M^1 (KUJC96619, 96620); 2 isolated M^2 (KUJC96738, 96739); 2 isolated M^3 (KUJC96496, 97021); 1 mandible without teeth (KUJC97020); 1 isolated M_1 (KUJC96380); 1 isolated M_2 (KUJC96858); 1 isolated M_3 (KUJC96980).
- Layer 12: 4 isolated M^1 (KUJC96615–96618); 3 isolated M^2 (KUJC96735–96737); 2 isolated M_1 (KUJC96379, 97019); 2 isolated M_2 (KUJC96856, 96857); 2 isolated M_3 (KUJC96978, 96979).
- Layer 13: 7 isolated M^1 (KUJC96608–96614); 7 isolated M^2 (KUJC96728–96734); 4 isolated M^3 (KUJC96492–96495); 1 mandible with M_1 (KUJC96371); 2 mandibles without teeth (KUJC97016, 97017); 8 isolated M_1 (KUJC96372–96378, 97018); 10 isolated M_2 (KUJC96846–96855); 6 isolated M_3 (KUJC96972–96977).
- Layer 14: 4 isolated M^1 (KUJC96604–96607); 6 isolated M^2 (KUJC96722–96727); 3 isolated M^3 (KUJC96489–96491); 1 mandible with I , M_1 , M_2 and M_3 (KUJC96367); 3 isolated M_1 (KUJC96368–96370); 6 isolated M_2 (KUJC96840–96845); 4 isolated M_3 (KUJC96968–96971).
- Layer 17: 5 isolated M^1 (KUJC96570–96574); 3 isolated M^2 (KUJC96690–96692); 8 isolated M^3 (KUJC96450–96457); 1 mandible with I , M_1 , M_2 and M_3 (KUJC96342); 1 mandible with M_1 and M_2 (KUJC96339); 1 mandible with M_3 (KUJC96939); 3 isolated M_1 (KUJC96340, 96341, 96343); 1 isolated M_2 (KUJC96806); 1 isolated M_3 (KUJC96940).
- Layer 18: 1 maxilla with M^1 (KUJC96569); 8 isolated M^1 (KUJC96561–96568); 10 isolated M^2 (KUJC96681–96689, 97009); 7 isolated M^3 (KUJC96443–96449); 3 isolated M_1 (KUJC96336–96338); 7 isolated M_2 (KUJC96799–96805); 6 isolated M_3 (KUJC96933–96938).
- Locality 1 of Ube Kosan Quarry
- Layer 4: 1 isolated M^3 (ASM 700044).
- Layer 3: 3 isolated M^1 (ASM 700045–700047); 1 isolated M^2 (ASM 700048); 1 isolated M_1 (ASM 700049); 4 isolated M_3 (ASM 700050–700053).
- Layer 2: 8 isolated M^1 (ASM 700054–700061); 5 isolated M^2 (ASM 700062–700066); 7 isolated M^3 (ASM 700067–700073); 14 isolated M_1 (ASM 700074–700087); 7 isolated M_2 (ASM 700088–700094); 10 isolated M_3 (ASM 700095–700104).
- Layer 1: 2 isolated M^1 (ASM 700105, 700106); 1 isolated M^3 (ASM 700107); 1 isolated M_1 (ASM 700108); 1 isolated M_3 (ASM 700109).

Origin of nomen — *japonicus*, Japan plus -icus (latin suffix), means a species known from Japan.

Type locality — Locality 3 of Ube Kosan Quarry, Mine, Yamaguchi Prefecture, west Japan (131°13'37"E, 34°10'32"N).

Geological distribution — Middle Pleistocene.

Geographical distribution — Japan; hitherto known only from west Honshu.

Diagnosis

Size smaller than that of *C. rufocanus*, but much and slightly larger than those of *C. rutilus* and *C. glareolus* respectively; postero-lateral bridge of palatine present; alveolus of M_3 forming a protuberant area on lingual face of horizontal ramus; time of root-formation later in life than those of *C. rutilus* and *C. glareolus* (it seems to be delayed with geological age). In M^1 and M^2 , isthmuses usually or almost always closed, and triangles well alternating; second minor fold considerably developed, but second secondary fold weakly developed or undeveloped. M^3 with three or four salient angles on lingual side, but usually three on buccal side; posterior loop variable in complexity, but simple morphotypes more frequently found (it seems to be changed with geological age); BRA1 generally deep, but shallower than BRA2. In M_1 , anterior loop elliptical in shape; LRA4 usually deep except in old individuals; Is 5 usually broadly open, so that T4 and T5 are usually confluent with each other. In M_2 and M_3 , first secondary fold weakly developed or undeveloped, while anterior labial fold usually undeveloped; Is 2 and Is 4 usually or always open.

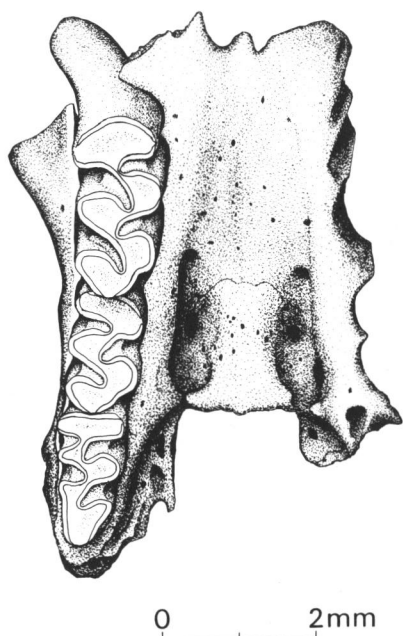


Fig. 102. *Clethrionomys japonicus*, sp. nov.
Holotype (KUJC96390). Ventral
view of maxillae and palatines.

Description

The materials of this species are obtained from the four localities listed above. Of these, Locality 3 of Ube Quarry exclusively yields adequate number of specimens for statistical analyses. In the subsequent description, the numbers given in parenthesis indicate the result of the analyses on the assemblage of this locality (total of all layers including "horizon unknown").

Skull —

Only the palatal region is preserved in a few specimens. The holotype, the best preserved specimen, is illustrated in Fig. 102. The incisive foramina terminate somewhat in front of the anterior border of the alveolus of M^1 . The anterior palatal foramina open at the inner side of either LSA3 or second minor fold of M^1 . The lateral palatal grooves begin at these foramina, and extend posteriorly to form wide depressed areas on both lateral sides of the palatines. The posterior palatal foramina open on the bottoms of the central parts of the grooves. The palato-maxillary suture runs through these foramina. The posterior edge of the palatines is rather straight, and the nasal spine is inconspicuous. Each of the lateral palatal grooves extends posteriorly to be a large duct which penetrates the dorsal side of the postero-lateral bridge of the palatine. The floor of this duct continues to a narrow lateral shelf observed on the inner side of M^3 .

M^1 —

M^1 comprises an anterior loop and four triangles. Therefore three salient angles are

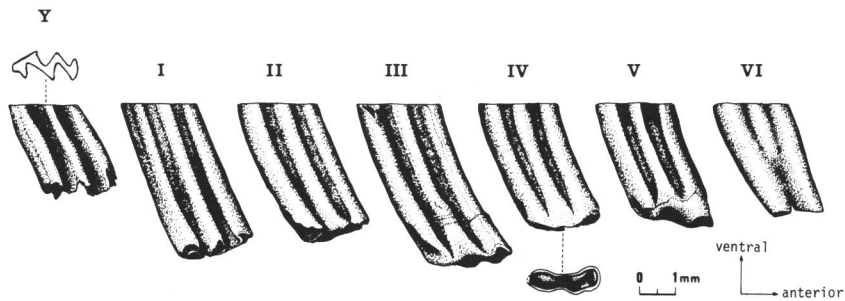


Fig. 103. *Clethrionomys japonicus*, sp. nov. Buccal view of left M^1 from Localities 1 and 3 of Ube Kosan Quarry showing the morphological characters of the age-classes Y to VI (occlusal and dorsal views are added in the age-classes Y and IV respectively).

Y, KUJC96528 from Layer 2 of Locality 3; I, KUJC96507 from Layer 1 of the same locality; II, KUJC96506 from Layer 1 of the same locality; III, KUJC96591 from Layer 8 of the same locality; IV, KUJC96540 from Layer 3 of the same locality; V, ASM 700045 from Layer 3 of Locality 1; VI, KUJC96539 from Layer 3 of Locality 3.

observed on both lingual and buccal sides. The anterior wall of the anterior loop is single-lobed in most specimens (93.9% of 115 specimens), while it is bilobed in the remaining specimens. The anterolingual conule is larger than or as large as the anterolabial conule in almost all the specimens. Each triangle is well alternating. All the isthmuses are usually closed (Table 33). The second minor fold is almost always represented by a weak concavity of the enamel wall. In a few specimens, this wall is straight, so that the second minor fold is not recognized (3.2% of 123 specimens). The buccal wall of T4 is sometimes straight (39.0% of 123 specimens), while it is slightly concave to form a weak second secondary fold in the remaining specimens.

The ontogenetic change in pattern is indistinct from the age-classes I to VI (Pls. 1–3). The basal part of LRA2 seems to be “closed” slightly earlier than those of BRA1, BRA2 and LRA1. The last three are “closed” nearly at the same time (Fig. 103).

M^2 —

M^2 is composed of an anterior loop and three triangles. Therefore two and three salient angles are observed on the lingual and buccal sides respectively. The anterior wall of the anterior loop is single-lobed in most specimens (96.0% of 124 specimens), while it is bilobed in the remaining specimens. All the isthmuses are closed in most specimens (Table 33). Each triangle is well alternating. The second minor fold is usually represented by a slight concavity of the enamel wall (87.3% of 126 specimens), but it is not recognized in the remaining specimens. The buccal wall of T4 is usually straight (72.8% of 125 specimens), while it is slightly concave in the remaining specimens.

The ontogenetic change in pattern is slight from the age-classes I to III (Pls. 4, 5). In the age-classes older than III, the specimens with rounded salient angles (for example 1, 5, 12 of Pl. 4) seem to be increased. The basal part of the second minor fold is already “closed” in the

Table 33. Frequency of closing of each isthmus in the upper molars of *Clethrionomys japonicus*, sp. nov. and the recent *C. rufocanus bedfordiae*. As regards the latter, the data on two different localities are cited from Aimi (1980). The number in each parenthesis indicates the total number of the examined specimens.

		<i>C. japonicus</i> Loc. 3 of Ube Kosan Quarry (total)	<i>C. rufocanus bedfordiae</i> (recent; by Aimi, 1980) Nopporo Shibechea	
M^1	Is 1	80.7% (114)	64.5% (203)	77.8% (27)
	Is 2	74.8 (123)	72.4 (203)	88.9 (27)
	Is 3	77.4 (124)	78.3 (203)	85.2 (27)
	Is 4	86.4 (125)	74.4 (203)	81.5 (27)
M^2	Is 2	98.2 (110)	91.1 (203)	88.9 (27)
	Is 3	97.2 (109)	91.6 (203)	92.6 (27)
	Is 4	93.6 (109)	86.2 (203)	88.9 (27)
M^3	Is 2	95.3 (106)	74.9 (203)	70.4 (27)
	Is 3	65.4 (107)	85.7 (203)	81.5 (27)
	Is 4	80.7 (109)	64.5 (203)	70.4 (27)
	Is 5	38.9 (108)	10.3 (203)	18.5 (27)

age-class I. Subsequently that of LRA2 is "closed." It is followed by the closing of the basal parts of BRA1 and BRA2 which takes place nearly simultaneously (Fig. 104).

M^3 —

M^3 is composed of an anterior loop, three triangles and a posterior loop. Three or four salient angles are observed on the lingual and buccal sides. The anterior wall of the anterior

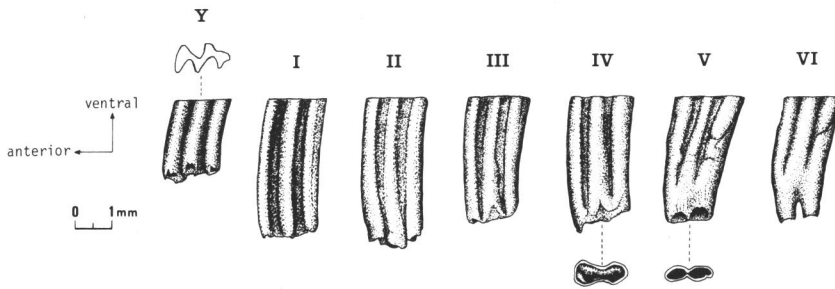


Fig. 104. *Clethrionomys japonicus*, sp. nov. Buccal view of right M^2 from Locality 3 of Ube Kosan Quarry showing the morphological characters of the age-classes Y to VI (occlusal and dorsal views are added in the age-classes Y, IV and V).

Y, KUJC96711 from Layer 9; I, KUJC96645 from Layer 1; II, KUJC96675 from Layer 4; III, KUJC96698 from Layer 10; IV, KUJC96697 from Layer 10; V, KUJC96656 from Layer 2; VI, KUJC96660 from Layer 2.

Table 34. Relationship between the age-class and morphotype in M^3 of *Clethrionomys japonicus*, sp. nov. from Locality 3 of Ube Kosan Quarry. The number of the specimens belonging to each age-class and each morphotype is tabulated.

AGE-CLASS	M O R P H O T Y P E					TOTAL
	S	L ₁	L ₂	C ₁	C ₂	
VI	2	1	—	—	—	3
VI-V	2	1	—	—	—	3
V	4	4	1	1	—	10
IV	6	1	—	2	2	11
IV-III	1	—	—	—	—	1
III	2	5	2	3	—	12
III-II	3	1	—	1	2	7
II	8	9	7	4	4	32
I-II	1	—	—	—	—	1
I	5	3	9	3	5	25
TOTAL	34	25	19	14	13	105

loop is usually single-lobed (76.9% of 108 specimens), while it is bilobed in the remaining specimens. BRA1 is usually deep, but shallower than BRA2. The frequencies of the closing of Is 2 and Is 4 are high, while that of Is 3 is lower (Table 33). Is 5 and Is 6 are often and

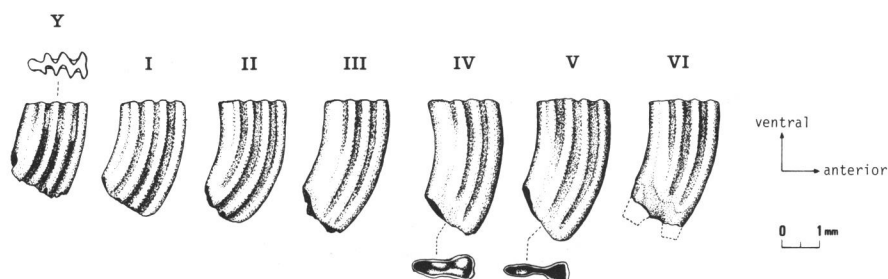


Fig. 105. *Clethrionomys japonicus*, sp. nov. Buccal view of left M^3 from Locality 3 of Ube Kosan Quarry showing the morphological characters of the age-classes Y to VI (occlusal and dorsal views are added in the age-classes Y, IV and V).

Y, KUJC96438 from Layer 4; I, KUJC96468 from Layer 9; II, KUJC96414 from Layer 2; III, KUJC96393 from Layer 1; IV, KUJC96392 from Layer 1; V, KUJC96473 from Layer 8; VI, KUJC96497 from Layer 6.

always open respectively. The triangles are generally alternating. In the specimens where Is 3 is open, however, T2 is opposite to T3 (for example, 6, 8, 15, 16 etc. in Pl. 6). T3 is always the largest among the triangles. T2 is larger or as large as T4. The posterior loop is highly variable in shape. The results of the morphotype analysis are shown in Table 34 and Fig. 114. Five morphotypes such as S, L₁, L₂, C₁ and C₂ are recognized, but F₁, F₂ and Ab are absent. The frequency of appearance is highest in the morphotype S (32.4% of 105 specimens), while it is lowest in the morphotype C₂ (12.4%).

Although the ontogenetic change in pattern is not so remarkable from the age-class I to VI, the frequencies of the simpler morphotypes seem to be increased with the growth of individuals (Pls. 6, 7; Table 34). It is related to the gradual disappearance of LRA4 and BRA4 in lateral view (Fig. 105). The basal parts of the re-entrant folds are generally "closed" in the following order (two re-entrant folds shown in a single parenthesis are "closed" nearly simultaneously): BRA4 (if present) → LRA4 → BRA3 → (LRA2, LRA3) → (BRA1, BRA2). The time gaps between the closing of LRA4 and that of BRA3 and between the closing of (LRA2, LRA3) and that of (BRA1, BRA2) are generally slight, so that the variation in this order is sometimes observed.

Mandible —

The horizontal ramus is more heavily built than that of *C. rutilus*, but more similar to that of *C. rufocanus*. Its lingual face is slightly concave antero-posteriorly and perforated by many small foramina. The symphyseal eminence is generally remarkable. Just above this eminence, a small prominence is always present on the lingual face of the horizontal ramus, but it varies in degree of development. The area between the alveoli and ascending ramus is rather wide and weakly depressed. However this depression is not so remarkable as in *Microtus*. The lower incisor passes the lingual side of M_2 , then shifts to the buccal side of M_3 . Because M_3 is displaced lingually by the passing of the incisor, its alveolus forms a remarkable protuberant area on the lingual face of the horizontal ramus. The capsule for the incisor on the lingual face of the ascending ramus is shorter and much weaker than that of *Microtus*. The

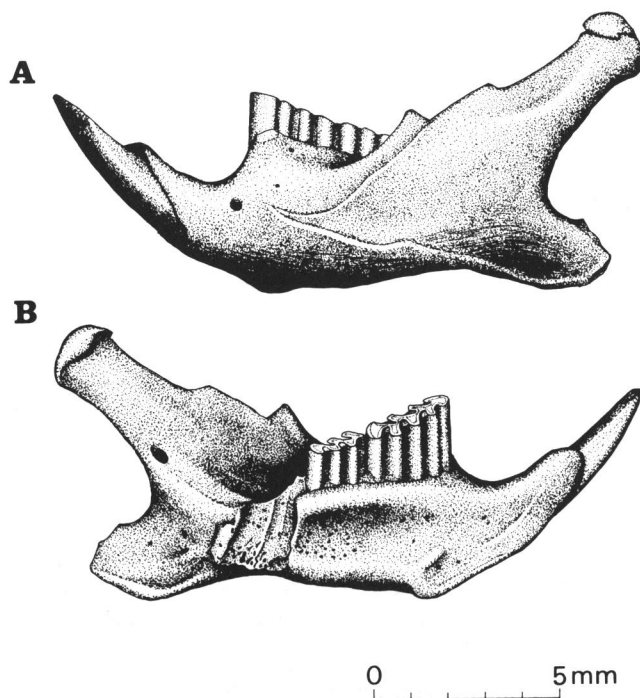


Fig. 106. *Clethrionomys japonicus*, sp. nov. Left mandible with I, M_1 and M_2 from Layer 4 of Locality 3 of Ube Kosan Quarry (paratype, ASM 700002). A, buccal view; B, lingual view.

mandibular foramen opens near the posterior border of the condylar process. The level of this foramen is only slightly higher than that of the occlusal surfaces of the lower molars.

The mental foramen opens on the buccal face of the horizontal ramus slightly anterior to the front margin of M_1 . The upper and lower masseteric crests are distinct. They begin at the same position which is below the anterior loop of M_1 . From this point, the former crest steeply ascends towards the base of the coronoid process, while the latter gradually descends posteriorly to reach the lower margin of the angular process. The anterior half of the buccal face of the condylar process is slightly concave. The condyle is narrowly ovate in dorsal view. The angular process is broad and short. It is somewhat broader than the condylar process.

M_1 —

M_1 comprises an anterior loop, five triangles and a posterior loop. Therefore five and four salient angles are observed on the lingual and buccal sides respectively. The anterior loop is generally elliptical. However it is sometimes confluent with T5 to form a wide dentine field. The results of the analysis on the variability of this part are given in Table 35 and Fig. 115. The morphotype 2 is most frequently found (47.7% of 86 specimens). The frequencies of the morphotypes 1 and 3 are considerably lower (29.1% and 16.3% respectively), and moreover

Table 35. Relationship between the age-class and morphotype in M_1 of *Clethrionomys japonicus*, sp. nov. from Locality 3 of Ube Kosan Quarry. The number of the specimens belonging to each age-class and each morphotype is tabulated.

AGE-CLASS	M O R P H O T Y P E				TOTAL
	1	2	3	4	
VI	—	—	1	2	3
V	—	1	—	—	1
V-IV	—	—	1	—	1
IV	1	4	1	1	7
IV-III	1	1	—	—	2
III	1	3	3	2	9
III-II	5	9	1	—	15
II	5	5	1	1	12
II-I	1	4	—	—	5
I	7	8	1	—	16
unknown	4	6	5	—	15
TOTAL	25	41	14	6	86

that of the morphotype 4 is lowest (7.0%). The anterior wall of the anterior loop is almost always single-lobed. In the age-class Y, however, it is rarely trilobed (for example, 29 of the age-class I+Y in Pl. 11). The anterolabial conulid is larger than or as large as the anterolingual conulid. The frequency of the "closed" isthmus is given in Table 36. Is 1 is always closed. The frequencies in Is 3 and Is 4 are somewhat lower (95.0% and 85.7% respectively). On the other hand, Is 2 is sometimes closed (only 37.3%). However, when this isthmus is decided as "open," it is mostly narrow (its width mostly less than 0.15 mm). In contrast to these, Is 6 is usually open, and moreover Is 5 is almost always open. T1, T2 and T3 are generally alternating. However T4 and T5 are mostly opposite to each other, and their dentine fields are usually confluent. The posterior wall of the posterior loop is always single-lobed.

The ontogenetic change in pattern can be observed in the anterior part of the crown (Table 35). In younger age-classes, the frequencies of the morphotypes 1 and 2 are high. In older age-classes, however, these morphotypes decrease, whereas the morphotypes 3 and 4 increase. Such a tendency indicates that LRA4 becomes shallower and Is 6 becomes broader with the growth of individuals. It is also coincident with the observation of the lingual side of the

Table 36. Frequency of closing of each isthmus in the lower molars of *Clethrionomys japonicus*, sp. nov. and the recent *C. rufocanus bedfordiae*. As regards the latter, the data on two different localities are cited from Aimi (1980). The number in parenthesis indicates the total number of the examined specimens.

		<i>C. japonicus</i> Loc. 3 of Ube Kosan Quarry (total)	<i>C. rufocanus bedfordiae</i> (recent; by Aimi, 1980)	
			Nopporo	Shibecha
M_1	Is 6	17.0% (94)	23.2% (203)	22.2% (27)
	Is 5	1.0 (97)	56.7 (203)	70.4 (27)
	Is 4	85.7 (98)	68.5 (203)	70.4 (27)
	Is 3	95.0 (100)	86.7 (203)	81.5 (27)
	Is 2	37.3 (99)	69.5 (203)	70.4 (27)
	Is 1	100.0 (99)	89.7 (203)	92.6 (27)
M_2	Is 4	3.5 (114)	0 (203)	0 (27)
	Is 3	100.0 (118)	94.1 (203)	92.6 (27)
	Is 2	16.1 (118)	27.1 (203)	51.9 (27)
	Is 1	100.0 (118)	97.5 (203)	96.3 (27)
M_3	Is 4	0 (106)	0 (203)	0 (27)
	Is 3	100.0 (107)	94.6 (203)	85.2 (27)
	Is 2	0 (108)	0 (203)	0 (27)
	Is 1	100.0 (108)	96.6 (203)	92.6 (27)

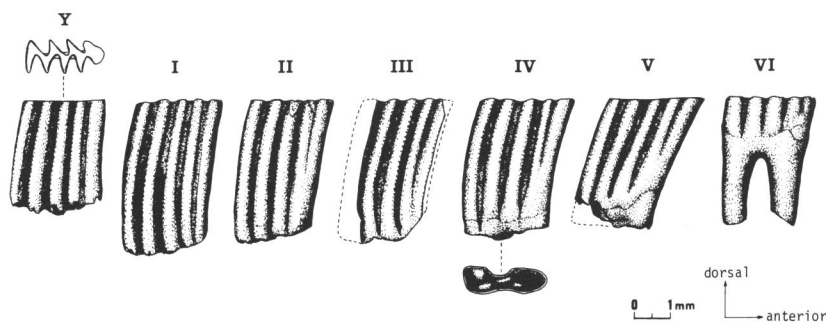


Fig. 107. *Clethrionomys japonicus*, sp. nov. Lingual view of left M_1 from Localities 1 and 3 of Ube Kosan Quarry showing the morphological characters of the age-classes Y to VI (occlusal and ventral views are added in the age-classes Y and IV respectively).

Y, KUJC96368 from Layer 14 of Locality 3; I, KUJC96309 from Layer 2 of the same locality; II, KUJC96304 from Layer 2 of the same locality; III, ASM 700077 from Layer 2 of Locality 1; IV, KUJC96283 from Layer 1 of Locality 3; V, KUJC96381 from Layer 6 of the same locality; VI, KUJC96316 from Layer 3 of the same locality.

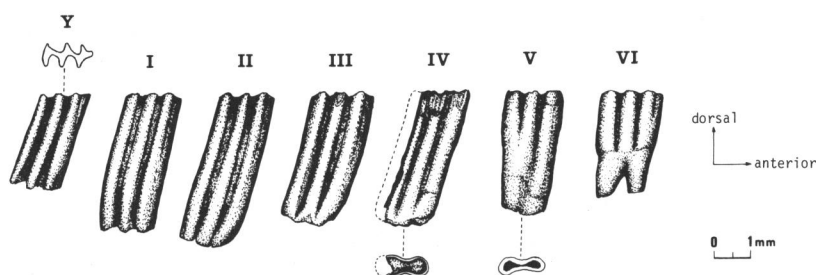


Fig. 108. *Clethrionomys japonicus*, sp. nov. Lingual view of left M_2 from Locality 3 of Ube Kosan Quarry, showing the morphological characters of the age-classes Y to VI (occlusal and ventral views are added in the age-classes Y, IV and V).

Y, KUJC96781 from Layer 2; I, KUJC96762 from Layer 1; II, KUJC96753 from Layer 1; III, KUJC96856 from Layer 12; IV, KUJC96780 from Layer 2; V, KUJC96803 from Layer 18; VI, KUJC96858 from Layer 11.

crown, where the basal part of LRA4 is first closed in younger age-classes (younger than the age-class II) and then this groove is gradually shortened and shallowed with growth.

The basal part of each re-entrant fold is closed in the following order: LRA4 → BRA3 → LRA3 → (LRA2, BRA2) → (LRA1, BRA1).

M_2 —

M_2 is composed of four triangles and a posterior loop. Therefore three salient angles are observed on both lingual and buccal sides. The first secondary fold is often represented by a concavity of the antero-lingual wall of T3 (58.2% of 134 specimens). The degree of its concavity is various, but mostly weak. In the remaining specimens, this fold is not recognized owing to the straightness of the wall. The antero-buccal wall of T4 is almost always straight (97.7% of 132 specimens). Is 4 is almost always open, while Is 1 and Is 3 are always closed (Table 36). Is 2 is usually open. Each triangle is generally alternating. However, when Is 4 is broadly open, T3 and T4 are opposite to each other (for example, 2, 3, 10 and 31 in Pl. 12).

And when Is 2 is broadly open, T2 is opposite to T1 (for example, 2, 3, 5, 15, 28 and 31 in Pl. 12). The posterior loop is always single-lobed.

The ontogenetic change in pattern is rather clearly observed (Pls. 12, 13). The first secondary fold and anterior labial fold are well developed in the age-class Y. However they soon become indistinct in the age class I. On the other hand, the triangles are arranged in opposite position in the age-class Y, but they become alternating in the age-classes I to III. As the individuals grow much older, the frequency of the specimens with opposite triangles becomes higher again.

The basal parts of LRA2, BRA2 and BRA1 are closed nearly simultaneously. The closing of the basal part of LRA1 takes place somewhat later.

M_3 —

M_3 is composed of two dentine fields and a posterior loop. Each dentine field is formed by the confluence of two neighbouring triangles. Therefore Is 2 and Is 4 are always open, while Is 1 and Is 3 are always closed (Table 36). Three salient angles are observed on both lingual and buccal sides. The lingual re-entrant angles are deeper than the buccal ones. The first secondary fold is sometimes represented by a slight concavity of the antero-lingual wall of T3. In the remaining specimens, however, this fold is not recognized. The anterior labial fold is never observed, because the antero-buccal wall of T4 is straight or somewhat convex. The posterior wall of the posterior loop is always single-lobed. The second minor fold and posteroconulid described in AIMI (1980) are never found.

Excepting the general tendency, the ontogenetic change in pattern is not so obvious (Pls. 14, 15). In the age-class Y, the first secondary fold and anterior labial fold are well developed. They soon disappear or become indistinct in the age-class I. The basal parts of BRA2 and BRA1 are first closed, which is followed by the closing of the basal part of LRA2. Soon after this, that of LRA1 is closed.

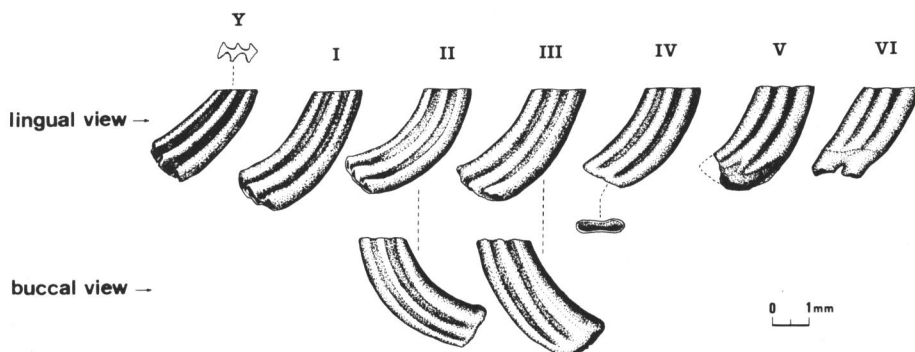


Fig. 109. *Clethrionomys japonicus*, sp. nov. Lingual and buccal views of left M_3 from Locality 3 of Ube Kosan Quarry, showing the morphological characters of the age-classes Y to VI (occlusal and ventral views are added in the age-classes Y and IV respectively).

Y, KUJC96902 from Layer 2; I, KUJC96894 from Layer 2; II, KUJC96892 from Layer 2; III, KUJC96981 from Layer 6; IV, KUJC96912 from Layer 3; V, KUJC96956 from Layer 8; VI, KUJC96911 from Layer 3.

Age structure of fossil assemblage

In the assemblage of Locality 3 of Ube Kosan Quarry, all the materials are classified into the age-classes in order to detect the age structure of the assemblage. The frequency of appearance of each age-class is calculated in each tooth kind (Fig. 110). Excepting M^3 , the tendency of appearance of each age-class is similar in each molar. Namely the age-class I is most frequently found, while the frequencies of older age-classes are much lower. The frequency of the specimens with roots and with sign of root-formation (age-classes older than I) ranges from 32.7% to 58.3%, when the specimens of age-class unknown are excluded. In addition, the appearance of the age-class Y is not rare (5.5–12.7% of the total specimens). On the other hand, the tendency of the appearance is considerably different in M^3 . Namely instead of the age-class I, II is most frequently found. The frequency of the specimens with roots and with sign of root-formation is remarkably higher (75.5%, in case the specimens of unknown age-class are excluded), while that of the age-class Y is very low (1.0% of the total specimens). These differences are possibly attributable to earlier root-formation of M^3 than in other molars.

Because the specimens from Locality 1 of Ube Kosan Quarry are not so abundant as those from Locality 3, the frequency of appearance of each age-class is calculated without distinction of tooth kind. In order to compare with this result, the frequency in Locality 3 is also calculated in the same manner (Fig. 111). The comparison of the age structure of these two assemblages indicates that the frequency of the specimens with roots and with sign of root-formation is considerably higher in Locality 1 than in Locality 3. This can be interpreted that the root-formation took place earlier in life in the population of Locality 1 than in that of Locality 3.

HASEGAWA *et al.* (1977) provided the data on the root-formation of M_1 of *C. japonicus* from Ando Quarry. They recognized three stages such as "pulp cavity open," "pulp cavity partly closed" and "root developed" in order to analyse the ontogenetic change in the pattern of M_1 . Because the last two stages approximately correspond to the age-classes IV, V and VI of the present paper, their data are comparable with those of Locality 3 of Ube Kosan Quarry. On the basis of the data of both localities, the frequency of these age-classes is much higher in Ando Quarry than in Locality 3. From this fact, it can be assumed that the frequency of the specimens with roots and with sign of root-formation is much higher in Ando Quarry than in Locality 3. On the other hand, in Locality 1 of Ube Kosan Quarry, the number of M_1 is too scarce to compare directly with these data. As demonstrated in the assemblage of Locality 3, however, the tendency of appearance of each age-class only in M_1 is generally consistent with that in the total of all kinds of molars (compare Fig. 110 with Fig. 111). The comparison of the data of Locality 1 with those of Ando Quarry indicates that the total frequency of the age-classes IV, V and VI is lower in the former locality than in the latter. Therefore it is also assumed that the frequency of the specimens with roots and with sign of root-formation is lower in Locality 1 than in Ando Quarry.

From the chronological viewpoints, the ages of the sediments of these three localities are somewhat different from each other. Namely that of Ando Quarry is considered to be earliest

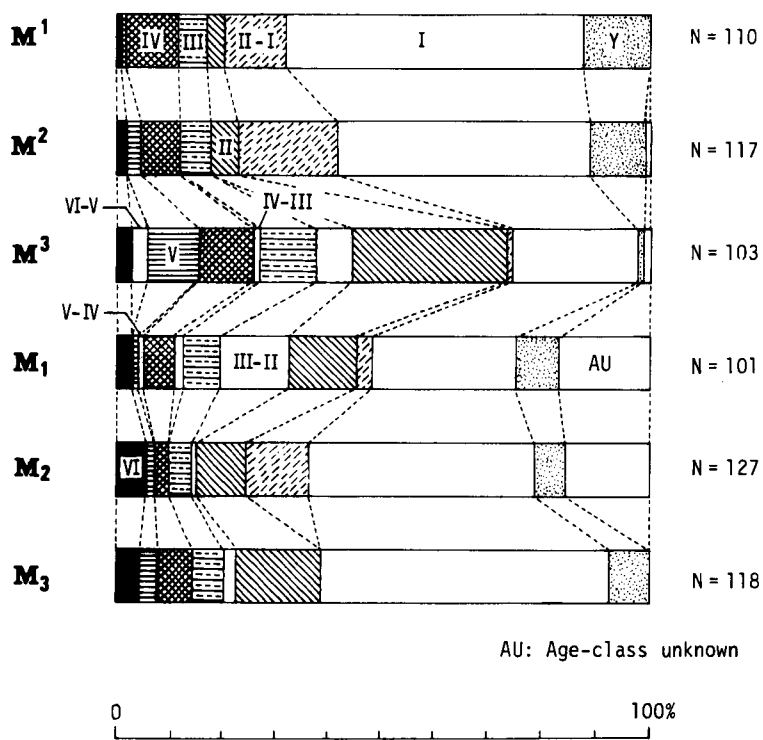


Fig. 110. Frequency of appearance of each age-class in the assemblage of *Clethrionomys japonicus*, sp. nov. from Locality 3 of Ube Kosan Quarry. The frequency is calculated in each kind of molar. N, number of examined specimens.

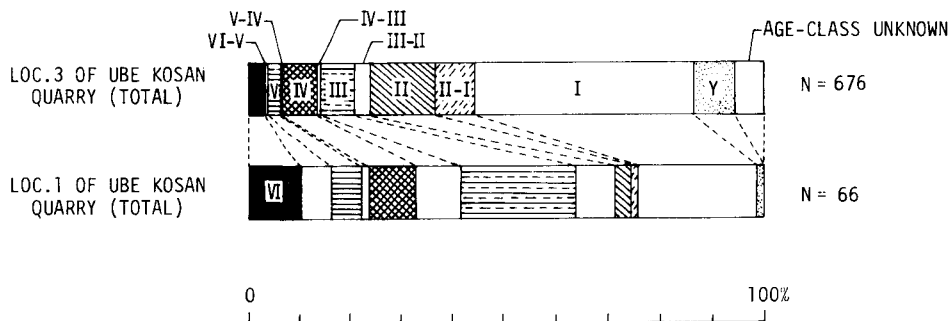


Fig. 111. Frequency of appearance of each age-class in the assemblages of *Clethrionomys japonicus*, sp. nov. from Localities 1 and 3 of Ube Kosan Quarry. All kinds of molar are put together. N, number of examined specimens.

of the three, while that of Locality 1 is equivalent to or somewhat earlier than that of the lower layers of Locality 3. Therefore the frequency of the specimens with roots and with sign of root-formation decreases from older to younger localities. Such a tendency can be interpreted as gradual delay of root-formation with geological age.

Measurements

The measurements of the mandibles and molars are given in Tables 37 and 38–43 respectively. In the case of the molars, the specimens belonging to the age-class Y are excluded as in other arvicolids, because they are much smaller than those belonging to older age-classes (Fig. 112). As shown in this figure, however, the size of the molars (occlusal length of crown) gradually increases with age even in the older age-classes than Y. Such a tendency is well coincident with the ontogenetic size change observed in the living *Clethrionomys rufocanus* (VIITALA, 1971; ABE, 1973). The size change is rather greater in M^1 , M^3 , M_1 and M_2 , whereas it is slighter in M^2 and M_3 .

Comparisons

The genus *Clethrionomys* is distributed throughout the northern part of the Holarctic Region. In the present North America, this genus is represented by a single species, *C. gapperi* (VIGORS). According to KURTÉN and ANDERSON (1980), this species is also the only representative of *Clethrionomys* in the Pleistocene of North America. Because this species strongly resembles the Palaearctic *C. rutilus* in molar pattern, it is easily distinguishable from the present fossils (see the subsequent comparison with *C. rutilus*). Therefore the Palaearctic forms of *Clethrionomys* are exclusively compared with the present fossils in the following part of this section.

Comparisons with the living species of Clethrionomys —

CORBET (1978) considered the following five species as the living components of the Palaearctic *Clethrionomys*:

Clethrionomys glareolus (SCHREBER, 1780)

Clethrionomys rutilus (PALLAS, 1779)

Clethrionomys rufocanus (SUNDEVALL, 1846)

Clethrionomys rex IMAIZUMI, 1971

Clethrionomys andersoni (THOMAS, 1905)

The last species including *niigatae* and *imaizumii* should be allocated to a different genus as several Japanese authors pointed out, because roots are never observed in its molars. In the present paper, it is considered to constitute the genus *Phaulomys* as well as *P. smithii*, as discussed in the subsequent section. On the other hand, the taxonomic status of *C. rex* is still controversial. ABE (1973, 1984) treated it as an independent species, while AIMI (1980) and HONACKI *et al.* (1982) synonymized it with *C. rufocanus*.

In comparison with the present fossils, *C. glareolus* has the following differential characters:

1. The size is somewhat smaller (based on the data given by VIRO and NIETHAMMER 1982, and the measurements of the recent specimens collected in Europe).

2. The crown is somewhat less hypsodont (the lateral view of the molars of *C. glareolus* with various ages is shown in RÖRIG and BÖRNER 1905, OGNEV 1950, and KOWALSKI and RUPRECHT 1981).
3. The time of root-formation is generally earlier in life (CORBET 1978 described that the development of root is visible in all but conspicuously juvenile animal in *C. glareolus* as well as in *C. rutilus*).

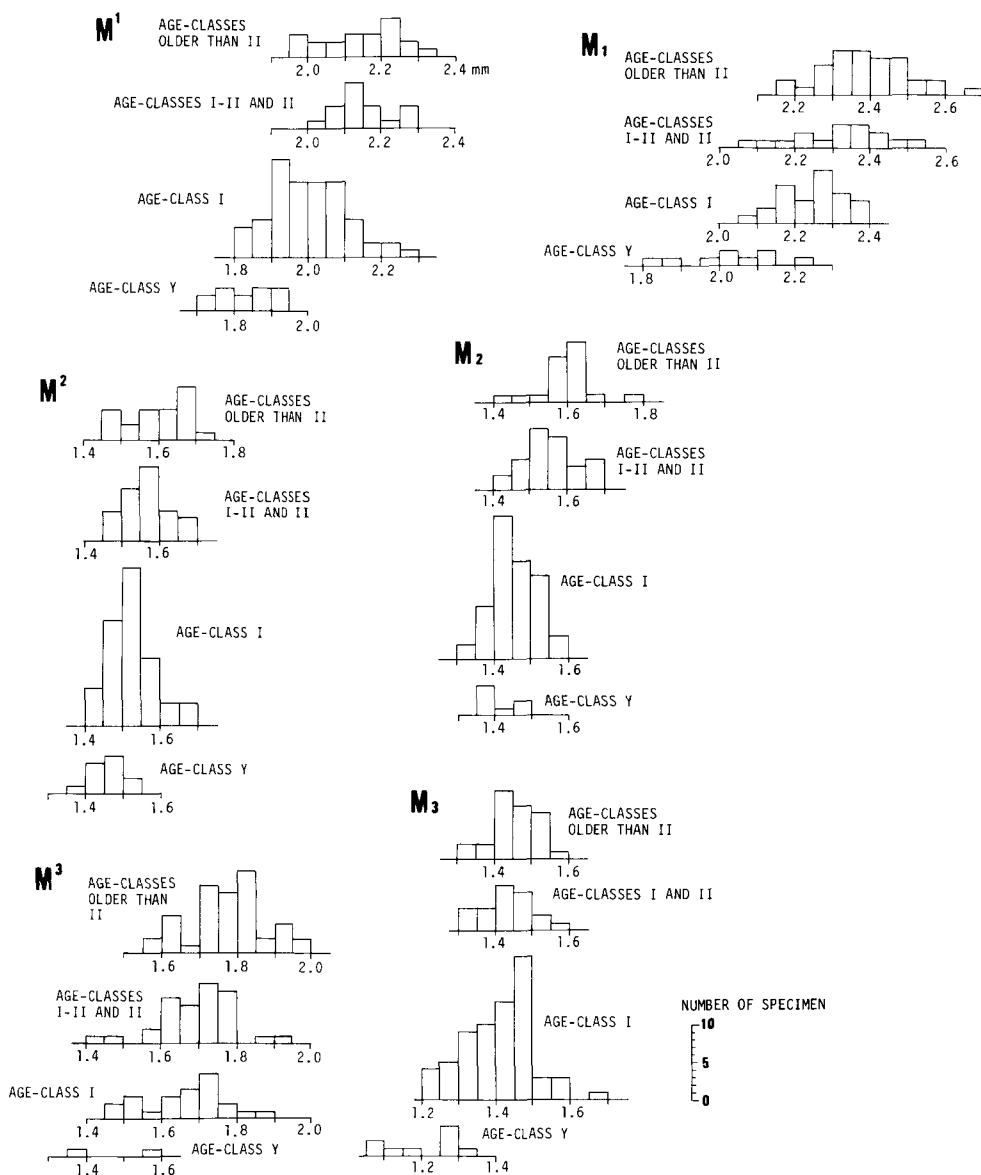


Fig. 112. Histogram showing the relationship between the length of crown and the age-class in the molars of *Clethrionomys japonicus*, sp. nov. from Locality 3 of Ube Kosan Quarry.

Table 37. Measurements of the mandibles of *Clethrionomys japonicus*, sp. nov. from Locality 3 of Ube Kosan Quarry in mm. The numbers on the left side correspond to those in Fig. 72.

	Horizon unknown		Layer 17	Layer 13	Layer 9	Layer 8	L a y e r 4							
	KUJC 96501	KUJC 96502	KUJC 96342	KUJC 96371	KUJC 97011	KUJC 96354	KUJC 96324	KUJC 96325	KUJC 96326	KUJC 96327	KUJC 96328	KUJC 96329	KUJC 96330	KUJC 96331
2. Total length of the mandible (id to the condyle)	—	—	—	—	—	—	14.97	—	—	—	—	—	—	—
3. Length from the tip of the incisor to the condyle	—	—	—	—	—	—	16.24	—	—	—	—	—	—	—
4. Length of the horizontal ramus	—	—	—	—	—	—	9.37±	—	—	—	—	—	—	—
5. Length of the diastema	—	—	—	—	—	—	3.58	—	—	—	—	—	—	—
6. Length of the ascending ramus (the posterior border of M ₃ to the condyle)	—	6.51±	—	—	—	—	6.45±	—	—	—	—	—	—	—
8. Height of the ascending ramus (gov to the highest point of the condyle)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10. Ditto (gov to the mandibular incision)	—	—	—	—	—	—	5.68±	—	—	—	—	—	—	—
12. Maximum height of the horizontal ramus	3.00	3.35	3.10	2.64±	2.93	3.13	3.23	3.05	3.07	2.71	3.10	3.16	2.79	3.37
14. Maximum thickness of the horizontal ramus	2.48	2.54	2.27	2.27	2.33	2.51	2.74	2.55	2.67	2.29	2.52	2.50	2.40	2.28
15. Length of the molar row (M ₁ to M ₃) at the crowns	5.39	—	5.51	—	—	—	—	—	5.63	5.18	5.22	—	—	—
16. Ditto at the alveoli	5.79	5.93±	6.03	—	—	—	5.58±	—	—	5.72±	—	—	—	—
17. Length of the molar row (M ₁ to M ₂) at the crowns	3.96	—	4.04	—	—	3.98	—	3.75	4.13	3.66	3.81	3.87	3.69	3.94
18. Ditto at the alveoli	3.99±	4.06±	4.13	4.04	—	—	4.00±	4.03±	—	4.01±	3.93	4.09	3.89±	3.85

Table 37. (Continued)

	Layer 4	Layer 3				Layer 2							Layer 1							
	ASM 70002	KUJC 96311	KUJC 96312	KUJC 96313	KUJC 96314	KUJC 96299	KUJC 96300	KUJC 96302	KUJC 96303	KUJC 96307	KUJC 96308	KUJC 97004	KUJC 96275	KUJC 96280	KUJC 96281	KUJC 96282	KUJC 96295	KUJC 96296	KUJC 96989	KUJC 96990
2.	14.34	—	—	—	—	—	—	—	—	—	—	—	—	14.97	—	—	—	—	—	—
3.	15.91	—	—	—	—	—	—	—	—	—	15.63	—	—	—	—	—	—	—	—	—
4.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.	3.46	—	—	3.47	—	—	—	—	—	3.67	—	—	—	3.58	—	—	—	—	—	—
6.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.	7.41	—	—	—	—	—	—	—	—	—	—	7.16	—	—	—	—	—	—	—	—
10.	5.86	—	—	—	—	—	—	—	—	—	—	5.77	—	—	—	—	—	—	—	—
12.	3.21	3.28	3.13	3.16	3.14	3.43	3.17	3.05	3.12	3.23	2.87	3.01	2.85	3.32	3.06±	3.20	2.95	2.92	2.95	3.13
14.	2.42	2.44	2.39	2.58	2.55	2.48	2.08	2.52	2.39	2.44	2.28	2.49	2.60	2.68	2.35	2.37	2.42	2.20	2.39	2.39
15.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.23	—	—	—	—
17.	4.15	4.01	4.10±	4.01	4.16	4.16	3.98	—	—	4.18	—	—	3.77	4.09	—	3.75	3.98	3.99	—	—
18.	4.12	4.06±	3.95	4.37	4.27±	4.18	4.01	4.10±	4.20±	4.12	3.97±	—	4.15	4.24±	4.19	4.18	4.16	4.26±	4.10	3.98

Table 38. Measurements of M^1 of *Clethrionomys japonicus*, sp. nov., and the recent *C. rufocanus bedfordiae* and *C. rutilus mikado* in mm. N, number of specimens; min, minimum; m, mean; max, maximum; SD, standard deviation (SD is calculated, when N is 5 and over).

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS (from Hokkaido)										
<i>C. rufocanus bedfordiae</i>	9	2.13	2.29	2.54	0.11	9	1.26	1.35	1.46	0.06
<i>C. rutilus mikado</i>	11	1.57	1.62	1.79	0.06	11	0.77	0.87	0.94	0.06
MIDDLE PLEISTOCENE (<i>C. japonicus</i>)										
Loc. 3 of Ube Kosan Quarry										
Horizon unknown	1	—	2.11	—	—	1	—	1.16	—	—
Layer 18	7	1.93	2.06	2.27	0.13	7	1.02	1.15	1.25	0.07
Layer 17	5	1.99	2.05	2.11	0.04	5	1.10	1.16	1.22	0.05
Layer 14	2	1.93	2.10	2.27	—	2	1.03	1.09	1.16	—
Layer 13	6	2.01	2.12	2.22	0.08	6	1.10	1.18	1.21	0.04
Layer 12	3	2.02	2.04	2.07	—	2	1.12	1.13	1.13	—
Layer 11	1	—	2.15	—	—	1	—	1.08	—	—
Layer 10	4	1.84	1.93	2.04	—	4	1.00	1.06	1.12	—
Layer 9	8	1.94	2.11	2.29	0.13	8	1.08	1.17	1.29	0.07
Layer 8	9	1.94	2.07	2.19	0.09	9	1.04	1.15	1.26	0.06
Layer 6	3	1.83	1.91	2.00	—	3	0.99	1.09	1.19	—
Layer 5	3	2.11	2.19	2.24	—	3	1.13	1.23	1.30	—
Layer 4	10	1.84	1.97	2.21	0.12	11	0.96	1.09	1.18	0.09
Layer 3	8	1.99	2.09	2.26	0.08	8	1.05	1.15	1.23	0.06
Layer 2	9	1.90	2.05	2.28	0.12	8	1.10	1.14	1.27	0.05
Layer 1	21	1.90	2.08	2.32	0.12	21	1.05	1.17	1.26	0.06
Loc. 1 of Ube Kosan Quarry										
Layer 3	1	—	2.09	—	—	2	1.01	1.07	1.14	—
Layer 2	5	1.95	2.07	2.13	0.07	5	1.03	1.09	1.17	0.05
Layer 1	2	2.14	2.19	2.25	—	2	1.09	1.15	1.22	—

Table 39. Measurements of M^2 of *Clethrionomys japonicus*, sp. nov., and the recent *C. rufocanus bedfordiae* and *C. rutilus mikado* in mm. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS (from Hokkaido)										
<i>C. rufocanus bedfordiae</i>	9	1.57	1.72	1.85	0.09	9	1.10	1.15	1.25	0.05
<i>C. rutilus mikado</i>	11	1.13	1.21	1.29	0.04	11	0.72	0.84	0.91	0.07
MIDDLE PLEISTOCENE (<i>C. japonicus</i>)										
Loc. 3 of Ube Kosan Quarry										
Horizon unknown	1	—	1.63	—	—	1	—	0.97	—	—
Layer 18	7	1.40	1.53	1.61	0.08	8	0.84	0.95	1.01	0.05
Layer 17	3	1.46	1.54	1.58	—	3	0.94	0.97	1.01	—
Layer 14	5	1.47	1.55	1.59	0.05	5	0.93	0.96	1.02	0.03
Layer 13	7	1.53	1.56	1.66	0.08	7	0.91	0.96	1.01	0.04
Layer 12	2	1.51	1.51	1.52	—	2	0.96	0.97	0.97	—
Layer 11	1	—	1.48	—	—	1	—	0.99	—	—
Layer 10	7	1.46	1.57	1.68	0.08	7	0.88	0.99	1.10	0.07
Layer 9	8	1.52	1.57	1.70	0.05	8	0.89	1.00	1.07	0.05
Layer 8	6	1.46	1.55	1.67	0.07	8	0.93	0.99	1.06	0.05
Layer 6	7	1.44	1.53	1.66	0.08	9	0.89	0.97	1.06	0.05
Layer 5	2	1.53	1.61	1.68	—	2	1.08	1.08	1.08	—
Layer 4	12	1.43	1.51	1.66	0.06	12	0.87	0.94	1.05	0.06
Layer 3	7	1.53	1.60	1.66	0.05	7	0.98	1.01	1.10	0.05
Layer 2	10	1.48	1.55	1.72	0.06	10	0.80	0.94	1.02	0.07
Layer 1	22	1.41	1.56	1.67	0.06	21	0.94	1.00	1.07	0.04
Loc. 1 of Ube Kosan Quarry										
Layer 2	3	1.51	1.59	1.68	—	4	0.99	1.02	1.03	—

Table 40. Measurements of M^3 of *Clethrionomys japonicus*, sp. nov., and the recent *C. rufocanus bedfordiae* and *C. rutilus mikado* in mm. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS (from Hokkaido)										
<i>C. rufocanus bedfordiae</i>	9	1.76	1.94	2.05	0.10	9	0.71	0.99	1.07	0.10
<i>C. rutilus mikado</i>	7	1.62	1.68	1.79	0.05	8	0.73	0.82	0.89	0.05
MIDDLE PLEISTOCENE (<i>C. japonicus</i>)										
Loc.3 of Ube Kosan Quarry										
Horizon unknown	1	—	1.78	—	—	1	—	0.86	—	—
Layer 18	2	1.46	1.57	1.68	—	3	0.77	0.79	0.81	—
Layer 17	8	1.68	1.72	1.81	0.10	8	0.81	0.83	0.87	0.05
Layer 14	1	—	1.79	—	—	1	—	0.80	—	—
Layer 13	4	1.63	1.77	1.99	—	4	0.74	0.78	0.83	—
Layer 11	1	—	1.56	—	—	1	—	0.79	—	—
Layer 10	9	1.62	1.72	1.82	0.08	9	0.78	0.85	0.90	0.04
Layer 9	5	1.49	1.76	1.94	0.16	5	0.71	0.83	0.91	0.08
Layer 8	14	1.54	1.74	1.90	0.11	15	0.73	0.84	0.94	0.06
Layer 6	2	1.58	1.66	1.73	—	2	0.84	0.84	0.85	—
Layer 4	7	1.56	1.72	1.94	0.12	7	0.67	0.81	0.92	0.08
Layer 3	10	1.64	1.76	1.89	0.07	10	0.79	0.86	0.95	0.05
Layer 2	14	1.43	1.71	1.95	0.14	13	0.71	0.84	0.95	0.06
Layer 1	24	1.51	1.72	1.91	0.10	25	0.74	0.85	0.95	0.05
Loc.1 of Ube Kosan Quarry										
Layer 4	1	—	1.62	—	—	1	—	0.85	—	—
Layer 2	1	—	1.64	—	—	2	0.74	0.78	0.81	—
Layer 1	1	—	1.68	—	—	1	—	0.92	—	—
Ikumo Quarry	1	—	1.66	—	—	1	—	0.82	—	—

Table 41. Measurements of M_1 of *Clethrionomys japonicus*, sp. nov., and the recent *C. rufocanus bedfordiae* and *C. rutilus mikado* in mm. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS (from Hokkaido)										
<i>C. rufocanus bedfordiae</i>	9	2.53	2.65	2.78	0.10	9	1.14	1.20	1.27	0.04
<i>C. rutilus mikado</i>	11	1.78	2.01	2.25	0.17	11	0.76	0.84	0.93	0.06
MIDDLE PLEISTOCENE (<i>C. japonicus</i>)										
Loc.3 of Ube Kosan Quarry										
Horizon unknown	1	—	2.32	—	—	1	—	1.11	—	—
Layer 18	3	2.39	2.42	2.52	—	3	1.00	1.03	1.05	—
Layer 17	4	2.30	2.39	2.52	—	5	1.00	1.06	1.17	0.06
Layer 15	1	—	2.16	—	—	1	—	0.84	—	—
Layer 14	—	—	—	—	—	1	—	0.87	—	—
Layer 13	8	2.25	2.34	2.50	0.08	8	0.93	0.99	1.06	0.05
Layer 12	—	—	—	—	—	1	—	1.12	—	—
Layer 11	1	—	2.43	—	—	1	—	1.03	—	—
Layer 10	5	2.26	2.32	2.41	0.07	5	0.92	0.99	1.11	0.07
Layer 9	4	2.40	2.48	2.56	—	4	1.05	1.07	1.09	—
Layer 8	9	2.07	2.32	2.84	0.21	9	0.94	1.01	1.10	0.05
Layer 6	6	2.25	2.40	2.66	0.14	6	1.00	1.06	1.16	0.05
Layer 5	2	2.28	2.42	2.57	—	3	1.03	1.04	1.06	—
Layer 4	11	2.17	2.31	2.45	0.09	12	0.88	1.02	1.17	0.07
Layer 3	9	2.16	2.34	2.53	0.11	9	0.77	1.02	1.15	0.10
Layer 2	8	2.17	2.37	2.55	0.13	9	0.94	1.02	1.10	0.05
Layer 1	21	2.08	2.28	2.49	0.11	21	0.91	1.01	1.11	0.06
Loc.1 of Ube Kosan Quarry										
Layer 3	—	—	—	—	—	1	—	1.00	—	—
Layer 2	8	2.14	2.29	2.45	1.00	12	0.85	0.95	1.06	0.06
Ikumo Quarry	1	—	2.34	—	—	1	—	0.99	—	—

Table 42. Measurements of M_2 of *Clethrionomys japonicus*, sp. nov., and the recent *C. rufocanus bedfordiae* and *C. rutilus mikado* in mm. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS (from Hokkaido)										
<i>C. rufocanus bedfordiae</i>	9	1.57	1.68	1.79	0.07	9	1.06	1.12	1.20	0.05
<i>C. rutilus mikado</i>	11	1.17	1.24	1.29	0.05	11	0.74	0.83	0.93	0.06
MIDDLE PLEISTOCENE (<i>C. japonicus</i>)										
Loc. 3 of Ube Kosan Quarry										
Horizon unknown	2	1.56	1.56	1.56	—	2	0.97	0.98	0.98	—
Layer 18	5	1.35	1.47	1.70	0.12	6	0.71	0.83	1.01	0.09
Layer 17	3	1.56	1.61	1.69	—	3	0.88	0.96	1.05	0.07
Layer 14	4	1.45	1.51	1.61	—	4	0.88	0.92	0.97	—
Layer 13	6	1.39	1.50	1.56	0.07	7	0.81	0.89	0.93	0.04
Layer 12	1	—	1.61	—	—	2	0.98	1.00	1.02	—
Layer 11	1	—	1.61	—	—	1	—	0.95	—	—
Layer 10	9	1.38	1.49	1.54	0.08	10	0.77	0.90	0.97	0.06
Layer 9	9	1.34	1.50	1.64	0.10	9	0.79	0.92	0.99	0.06
Layer 8	10	1.38	1.46	1.52	0.05	11	0.77	0.88	0.97	0.06
Layer 6	5	1.45	1.53	1.64	0.07	5	0.92	0.96	1.02	0.04
Layer 5	2	1.55	1.56	1.56	—	2	0.90	0.94	0.97	—
Layer 4	18	1.32	1.49	1.59	0.07	18	0.74	0.90	1.06	0.08
Layer 3	11	1.37	1.55	1.68	0.09	11	0.88	0.95	1.05	0.06
Layer 2	14	1.41	1.55	1.79	0.10	14	0.82	0.91	1.06	0.06
Layer 1	22	1.41	1.51	1.65	0.07	23	0.86	0.92	1.02	0.04
Loc. 1 of Ube Kosan Quarry										
Layer 2	1	—	1.42	—	—	3	0.82	0.87	0.94	—
Ikumo Quarry	1	—	1.66	—	—	1	—	1.02	—	—

Table 43. Measurements of M_3 of *Clethrionomys japonicus*, sp. nov., and the recent *C. rufocanus bedfordiae* and *C. rutilus mikado* in mm. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS (from Hokkaido)										
<i>C. rufocanus bedfordiae</i>	9	1.49	1.62	1.72	0.07	9	0.86	0.92	0.99	0.04
<i>C. rutilus mikado</i>	7	1.18	1.25	1.31	0.05	7	0.71	0.80	0.95	0.07
MIDDLE PLEISTOCENE (<i>C. japonicus</i>)										
Loc. 3 of Ube Kosan Quarry										
Horizon unknown	4	1.39	1.45	1.58	—	4	0.73	0.77	0.80	—
Layer 18	5	1.25	1.40	1.52	0.11	6	0.64	0.75	0.85	0.08
Layer 17	3	1.47	1.54	1.68	—	3	0.74	0.79	0.87	—
Layer 14	3	1.43	1.46	1.48	—	4	0.70	0.75	0.82	—
Layer 13	6	1.21	1.38	1.46	0.09	6	0.61	0.69	0.71	0.04
Layer 12	2	1.50	1.52	1.53	—	2	0.81	0.82	0.83	—
Layer 11	1	—	1.41	—	—	1	—	0.79	—	—
Layer 10	6	1.27	1.41	1.50	0.10	7	0.68	0.73	0.78	0.03
Layer 9	6	1.34	1.43	1.57	0.08	7	0.70	0.74	0.77	0.03
Layer 8	9	1.33	1.42	1.56	0.08	10	0.67	0.75	0.79	0.04
Layer 6	5	1.29	1.43	1.51	0.08	5	0.63	0.74	0.80	0.06
Layer 5	1	—	1.45	—	—	1	—	0.75	—	—
Layer 4	14	1.21	1.42	1.55	0.08	14	0.63	0.74	0.83	0.06
Layer 3	10	1.24	1.46	1.53	0.08	10	0.65	0.76	0.82	0.04
Layer 2	14	1.30	1.39	1.51	0.06	14	0.68	0.72	0.76	0.03
Layer 1	24	1.30	1.42	1.59	0.07	24	0.62	0.72	0.82	0.05
Loc. 1 of Ube Kosan Quarry										
Layer 3	—	—	—	—	—	1	—	0.77	—	—
Layer 2	5	1.27	1.36	1.47	0.07	5	0.62	0.67	0.72	0.04
Layer 1	1	—	1.27	—	—	1	—	0.66	—	—
Ikumo Quarry	2	1.29	1.33	1.37	—	2	0.59	0.67	0.75	—

4. BRA1 of M^3 is somewhat shallower (this character of *C. glareolus* was described by MILLER, 1912).
5. The frequencies of appearance of the complicate morphotypes (C_1 and C_2) are higher in M^3 . ZEJDA (1960) described the simplification of the pattern with age in *C. glareolus*. However the pattern is relatively constant in his age-groups I to III (roots of M_1 shorter than 1mm) where the complicate morphotypes appear in ca 75% of the total specimens. Because almost all the specimens of the present fossils belong to these age-groups, their frequency is decidedly lower in the present fossils than in *C. glareolus*.
6. In M_1 , LRA4 is usually shallow and Is 6 is broadly open, so that the morphotypes 3 and 4 are usually found (the morphotypes 1 and 2 are usually found in the present fossils).
7. T1 and T2 as well as T3 and T4 are usually confluent with each other in M_1 (these triangles are usually separated from each other in the present fossils).

CORBET (1978) considered *centralis* (= *frater*) from Tien Shan Mts as a synonym of *C. glareolus*, but he also wrote the possibility that it was a distinct species. On the other hand, Russian authors generally gave it specific rank (see HONACKI *et al.*, 1982). On the basis of the description and illustrations given by OGNEV (1950), *centralis* differs from the present fossils in the following characters:

1. BRA1 of M^3 is shallower.
2. The anterior loop is always confluent with T5 to form a large dentine field in M_1 (the anterior loop is more independent in the present fossils).
3. LRA4 of M_1 is absent or very shallow (it is better developed in the present fossils).
4. T1 and T2 as well as T3 and T4 are opposite and well confluent with each other in M_2 (they are more alternating in the present fossils).
5. The buccal re-entrant angles of M_3 are much shallower in grown individuals.

C. rutilus is easily distinguishable from the present fossils by the following characters:

1. The size is decidedly smaller (Tables 38–43).
2. The postero-lateral bridge of the palatine is not formed (it is formed in the present fossils).
3. The alveolus of M_3 does not form a protuberant area on the lingual face of the horizontal ramus (it is remarkable in the present fossils).
4. The horizontal ramus is slenderer.
5. The time of root-formation is earlier in life.
6. The salient angles are more acutely pointed, and the enamel walls of the triangles are generally straight, so that each triangle shows more triangular appearance.
7. The isthmuses of the upper molars tend to be uniformly open, but their width is not broad (they are generally closed in the present fossils).
8. The second minor fold and second secondary fold are always undeveloped in M^1 and M^2 (they are more or less developed in the present fossils).
9. The anterior loop of M^3 is more rectangular.
10. BRA1 is nearly as deep as BRA2 in M^3 (the former is shallower than the latter in the present fossils).
11. The posterior loop of M^3 is almost always complicate (the frequencies of the complicate morphotypes such as C_1 , C_2 , F_1 and F_2 are much lower in the present fossils).
12. M^3 is generally longer than M^1 (M^3 is shorter than M^1 in the present fossils).
13. The buccal part of the anterior loop of M_1 is strongly elongated postero-buccally, and its tip (BSA4) is sharply pointed (such elongation is inconspicuous, and BSA4 is rounded in the present fossils).
14. T2 and T4 extend more posteriorly in M_1 .
15. The first secondary fold and anterior labial fold of M_2 and M_3 are always undeveloped (they are more or less developed in the present fossils).
16. M_2 and M_3 are broader.

The osteological and dental characters of *C. rufocanus* were described by many authors

(MILLER, 1912; HINTON, 1926; TOKUDA, 1941b; OGNEV, 1950; STORCH *et al.*, 1973; HENTTONEN and VIITALA, 1982 etc.). Additionally the dental characters of the subspecies of Hokkaido (*C. rufocanus bedfordiae*) were analysed in detail by ABE (1973) and AIMI (1980). Besides these data, many recent specimens of this subspecies are directly observed in the present study. As the result, the following differences are recognized between *C. rufocanus* and the present fossils:

1. *C. rufocanus* is obviously larger than the present fossils (Tables 38–43).
2. The second secondary fold of M^1 and M^2 is better developed in *C. rufocanus*.
3. As regards the posterior loop of M^3 , the complicate morphotypes such as C_1 , C_2 , F_1 and F_2 are generally less frequently found in *C. rufocanus*.
4. As regards the anterior part of M_1 , the morphotypes 3 and 4 are less frequently found in *C. rufocanus* (except very old individuals; cf. Tables 4 and 5 of ABE, 1973).
5. Is 2 and Is 5 of M_1 are more frequently closed in *C. rufocanus* (Table 36).
6. T4 and T5 of M_1 are alternating in *C. rufocanus* (these triangles are opposite to and confluent with each other in the present fossils).
7. The first secondary fold of M_2 and M_3 , and the anterior labial fold of M_2 are better developed in *C. rufocanus*.

The Korean form, *regulus*, is generally regarded as a subspecies of *C. rufocanus*. Recently CORBET (1978) transferred it to *Eothenomys*. According to him, its molars stop growing in old animals, but do not form multiple roots. The observation of 20 recent specimens* by the present author shows that this form is distinct from the present fossils in having characteristic patterns of M^3 (posterior loop generally elongated and slender; LSA5 usually present, but much smaller than LSA4) and of M_1 (anterior loop more triangular; BSA4 remarkably elongating postero-buccally; vestigial BRA4 sometimes present; LRA4 always deep; Is 2 and Is 5 almost always closed) besides the characters 1, 2 and 6 of *C. rufocanus* listed above.

C. rex is closely related or conspecific with *C. rufocanus*. According to IMAIZUMI (1971), it is characterized by large size, incomplete postero-lateral bridge of palatine, complicate M^3 and symmetrical anterior loop of M_3 . However AIMI (1980) doubted the validity of these characters. At any rate, these characters are not coincident with those of the present fossils.

Comparisons with the fossil species of Clethrionomys —

Several fossil species of *Clethrionomys* have been described from the Pliocene and Pleistocene sediments of Europe. They are:

Clethrionomys acrorhiza KORMOS, 1933

Clethrionomys erli BRUNNER, 1936

Clethrionomys esperi (HELLER, 1930)

Clethrionomys hintonianus KRETZOI, 1958

Clethrionomys kretzoi (KOWALSKI, 1958)

Clethrionomys rufocanoides STORCH, FRANZEN et MALEC, 1973

Clethrionomys sebaldi HELLER, 1963

Besides these, *C. harrisoni* and *C. kennardi* were described from the British Quaternary by HINTON (1926). However these species were synonymized with *C. glareolus* by SUTCLIFFE and KOWALSKI (1976).

According to KORMOS (1933), *C. acrorhiza* is characterized by the passing position of the

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lower incisor under the lower molars. Namely, KORMOS described that the incisor passed from the lingual to buccal sides between the anterior and posterior roots of M_2 in this species ("Firstenwurzlerstellung"), although it passed the lingual side of M_2 in other species of *Clethrionomys* ("Seitenwurzlerstellung"). The present fossils are referable to "Seitenwurzlerstellung." However this character seems to be overestimated, because "Firstenwurzlerstellung" is found in aged individuals of *C. glareolus* (STORCH *et al.*, 1973). The molar pattern of *C. acrothiza* is very similar to that of *C. glareolus*. Therefore it is distinct from the present fossils. Moreover the measurements given by KORMOS (1933) and HELLER (1958) indicate that *C. acrothiza* is considerably smaller than the present fossils.

C. erli is nearly as large as the present fossils. The pattern of M_1 of this species shown by BRUNNER (1936, 1949, 1957) is abnormal as a species of *Clethrionomys*. Namely the anterior loop is broadly confluent not only with T4 but also with T5. LRA4 and BRA3 are usually shallow or absent. In the present fossil assemblages, only one M_1 from Locality 1 of Ube Kosan Quarry (17 of Pl. 9) is somewhat similar to some variants of *C. erli* illustrated by BRUNNER (Abb. 6 of 1936; Abb. 5 of 1949). However almost all the specimens of the present fossils are clearly different from this species.

C. esperi is diagnosed by triangular anterior loop and pointed LSA5 in M_1 (HELLER 1930). On the other hand, the anterior loop is generally elliptical and LSA5 is blunter in the present fossils. Each isthmus of M_2 and M_3 tends to be closed in *C. esperi*, while Is 2 and Is 4 of the same teeth are usually or always open in the present fossils (Table 36). Moreover the buccal re-entrant angles of M_3 seem to be deeper in *C. esperi*. As regards the size of molars, *C. esperi* is somewhat smaller than the present fossils in M_1 , but as large as the latter in M_2 and M_3 .

C. hintonianus was originally described as *C. hintoni* by KORMOS (1934), and subsequently emended by KRETZOI (1958). According to the original description and illustration given by KORMOS, this species is well coincident with the present fossils in size and general pattern of lower molars. However the following differences are also observed:

1. The anterolingual conulid is clearly larger than the anterolabial conulid in M_1 of *C. hintonianus*, while the former is generally as large as or smaller than the latter in the present fossils.
2. LRA4 of M_1 is wider and deeper in *C. hintonianus*.
3. The relative size of the buccal triangles against the lingual ones is smaller in M_2 of *C. hintonianus*.

C. kretzoi was first described as a new species of *Dolomys* by KOWALSKI (1958). Subsequently KOWALSKI (1964) and STORCH *et al.* (1973) treated it as a species of *Clethrionomys*. The molars of this species have several primitive characters. Namely, the molars are well rooted, and the cementum in the re-entrant angles is scarce or lacking. The triangles are more or less confluent with each other. They are also confluent with the anterior and posterior loops in M_1 and with the posterior loop in M_2 . M_2 shows a symmetrical pattern. These characters are generally inconsistent with those of the present fossils. Exceptionally very young individuals of the present fossils sometimes show a similar pattern, but they are, of course, unrooted. Therefore *C. kretzoi* is easily distinguishable from the present fossils.

The dental characters of *C. rufocanoides* are given by STORCH *et al.* (1973). In comparison with the present fossils, M_1 of *C. rufocanoides* differs in having closed Is 5, thicker enamel band,

slightly larger size and lower crown-height.

According to the description and illustration given by HELLER (1963), M_1 of *C. sebaldi* shows the pattern which is often observed in young individuals of other species of *Clethrionomys*. Namely, the triangles are broadly confluent with each other, and each salient angle is sharply pointed. The cementum in the re-entrant angles is poorly developed. HELLER, however, mentioned that this M_1 was rooted. On the other hand, several young individuals of the present fossils resemble this M_1 in pattern, but they never show any sign of root-formation. Therefore the present fossils are distinguishable from *C. sebaldi*. HELLER (1963) also described that M_1 of *C. sebaldi* had an anterior loop with characteristic rhombic shape. However the anterior loop with similar shape is observed in some variants of the present fossils. *C. sebaldi* is nearly as large as the present fossils in accordance with the measurements by HELLER (1963) and STORCH *et al.* (1973).

Comparisons with the fossil Clethrionomys known from East Asia —

Among the fossils from East Asia, those from Locality 1 of Choukoutien and Ku-hsiang-tung are comparable with the present fossils. The description and illustration given by YOUNG (1934) clearly indicate that the Choukoutien form is rather similar to *C. rufocanus* than to the present fossils in having closed Is 2 and Is 5 in M_1 and closed Is 2 in M_2 . Of two specimens from Ku-hsiang-tung described by TOKUDA (1939), the larger one is different from the present fossils in having larger size, and closed or narrow isthmuses (especially Is 5 of M_1 , and Is 2 and Is 4 of M_2). The smaller one is well coincident with the present fossils in size. However it is characterized by acutely pointed salient angles, regularly triangular triangles, and postero-buccal extension of BSA2, 3 and 4 of M_1 . These characters recall *C. rutilus* instead of the present fossils. Consequently both of the Choukoutien and Ku-hsiang-tung forms are distinguishable from the present fossils in dental characters.

Discussion

Because the fossil arvicolids other than *Microtus* occurring in the Middle Pleistocene localities of Honshu show uniformity in size and in osteological and dental characters, they are assignable to a single species. The above-mentioned comparisons indicate that this species is distinguishable from all the living and fossil species of *Clethrionomys* hitherto known. Therefore it can be regarded as a new species, which is named *C. japonicus* here. Previously, KOWALSKI and HASEGAWA (1976) identified it as *C. rufocanus*, while HASEGAWA *et al.* (1977) pointed out its special similarity to *C. centralis* (= *frater*). However these opinions are obviously unacceptable from the detailed analyses of the fossil populations and the comparisons given above.

Among the living species of *Clethrionomys*, *C. japonicus* is rather similar to *C. glareolus*, *C. centralis* and *C. rufocanus* than to *C. rutilus*. *C. glareolus* is possibly closely related to *C. centralis*, while *C. japonicus* show the intermediate characters between these two species and *C. rufocanus*. The phylogenetic relationship of these species are provisionally given in Fig. 113. *C. japonicus* possibly evolved along a lineage independent from *C. glareolus* and *C. rufocanus*, although these species possibly share a single ancestor of the Early Pleistocene or Pliocene.

Among the fossil species of *Clethrionomys*, the lower molars of *C. hintonianus* show great

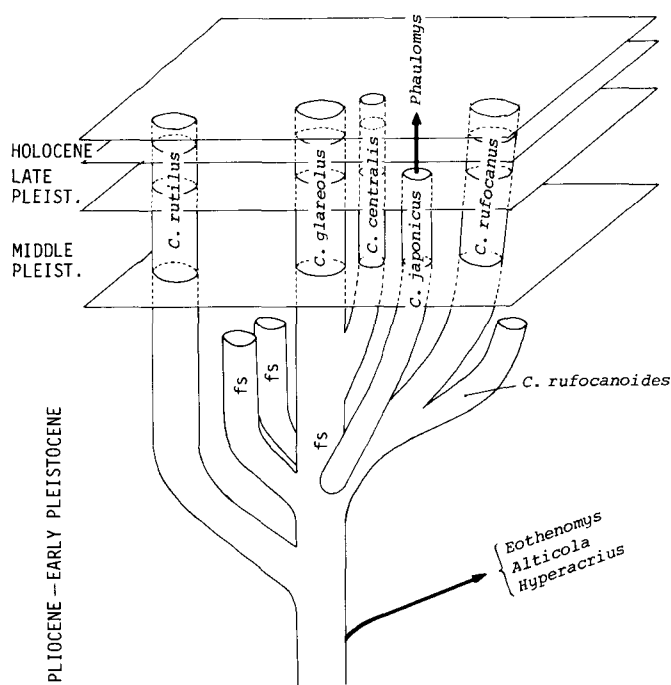


Fig. 113. Phylogeny of the species of *Clethrionomys* provisionally proposed in this paper. fs, Early Pleistocene fossil species of *Clethrionomys* related to *C. glareolus*.

similarity to those of *C. japonicus*. This Early Pleistocene species might be near to the lineage of *C. japonicus*. Unfortunately, the upper molars of this species can not be compared owing to the lack of the available information. Therefore the relationship between these two species still remains in question.

C. japonicus flourished in the Middle Pleistocene of Honshu, and is assumed to have been well adapted to the temperate forests of this island. This species or its ancestral form possibly migrated from the continent in the Early Pleistocene or the earlier part of the Middle Pleistocene. In China, the fossil records of *Clethrionomys* are completely absent from the Early Pleistocene sediments and very rare in the Middle Pleistocene sediments (only from Choukoutien and Miaohoushan; Table 32). As already mentioned, the Choukoutien form is identified as *C. rufocanus*, and not related to *C. japonicus*. Therefore the migration route of *C. japonicus* or its ancestral form from North China is not acceptable. The route should be considered more northwardly (possibly from Transbaikalia to Honshu).

***Clethrionomys-Phaulomys* transitional form**

(Figs. 116, 124; Pls. 1, 4, 6, 7, 9-12, 14, 16, 17)

Synonym —

Clethrionomys rufocanus SUNDEVALL; KOWALSKI and HASEGAWA 1976 (in part), *Bull. Nat. Sci. Mus. Ser. C*, **2**, 48-52; from Shiriya Quarry, Miyata First Cave (?), Miyata Second Cave and Shiraiwa Mine (?).

- Eothenomys smithi* (THOMAS); KOWALSKI and HASEGAWA 1976 (in part), *Ibid.*, Ser. C, **2**, 51–53; from Miyata Second Cave.
- Aschizomys andersoni* (THOMAS); KOWALSKI and HASEGAWA 1976 (in part), *Ibid.*, Ser. C, **2**, 53–54; from Shiriya Quarry.
- Clethrionomys* sp.; KAWAMURA 1977, *Fossil Club Bull.*, (14), 7; from Kumaishi-do Cave.
- Eothenomys smithi* (THOMAS); KAWAMURA 1977, *Ibid.*, (14), 7; from Kumaishi-do Cave.
- Clethrionomys* sp.; KAWAMURA and KAJIURA 1980, *Jour. Speleol. Soc. Japan*, **5**, 53, 60–61; from Sugi-ana Cave.
- Eothenomys* sp.; KAWAMURA and KAJIURA 1980, *Ibid.*, **5**, 53; from Sugi-ana Cave.
- Clethrionomys* cf. *rufocanus* (SUNDEVALL); OKUMURA *et al.* 1982, *Earth Sci.*, **36**, 216; from Kumaishi-do Cave.
- Eothenomys* sp.; OKUMURA *et al.* 1982, *Ibid.*, **36**, 216; from Kumaishi-do Cave.

Materials —

Sugi-ana Cave

1 fragmental skull with M¹, M² and M³ (KUJC98138); 1 maxilla with M¹, M² and M³ (KUJC98139); 2 maxillae with M¹ and M² showing sign of root-formation (KUJC98104, 98137); 4 maxillae with M¹ and M² (KUJC98140–98143); 12 maxillae with M¹ (KUJC98144–98155); 1 maxilla with M² (KUJC98156); 1 maxilla without teeth (KUJC98157); 2 mandibles with I, M₁, M₂ and M₃ (KUJC98158, 98159); 1 mandible with M₁, M₂ and M₃ (KUJC98160); 15 mandibles with I, M₁ and M₂ (KUJC98161–98175); 9 mandibles with M₁ and M₂ (KUJC98176–98184); 2 mandibles with M₂ and M₃ (KUJC98185, 98186); 1 mandible with I and M₁ (KUJC98187); 3 mandibles with I and M₂ (KUJC98188–98190); 1 mandible with I and M₃ (KUJC98191); 1 mandible with M₁ showing sign of root-formation (KUJC98080); 7 mandibles with M₁ (KUJC98192–98198); 4 mandibles with M₂ (KUJC98199–98202); 12 isolated M¹ with roots or sign of root-formation (KUJC98101–98103; 98105–98111, 98135, 98136); 431 isolated M¹ without sign of root-formation (KUJC98203–98633); 8 isolated M² with roots or sign of root-formation (KUJC98112–98118, 98120); 312 isolated M² without sign of root-formation (KUJC98119, 98634–98944); 14 isolated M³ with roots or sign of root-formation (KUJC98087–98100); 233 isolated M³ without sign of root-formation (KUJC98945–99177); 19 isolated M₁ with roots or sign of root-formation (KUJC98067–98079, 98081–98086); 378 isolated M₁ without sign of root-formation (KUJC99178–99555); 5 isolated M₂ with roots or sign of root-formation (KUJC98121–98125); 284 isolated M₂ without sign of root-formation (KUJC99556–99839); 9 isolated M₃ with roots or sign of root-formation (KUJC98126–98134); 200 isolated M₃ without sign of root-formation (KUJC99840–100039).

F₃ of Kumaishi-do Cave

1 mandible with I, M₁, M₂ and M₃ (YKS 04006); 1 mandible with I, M₁ and M₂ (YKS 04001); 1 mandible with I (YKS 04020); 2 mandibles without teeth (YKS 04012, 04021); 11 isolated M¹ without sign of root-formation (YKS 04145, 04150, 04162, 04166, 04301–4307); 21 isolated M² without sign of root-formation (YKS 04183–04186, 04191, 04207, 04214, 04222, 04278, 04308–04319); 20 isolated M³ without sign of root-formation (YKS 04075, 04077, 04078, 04082, 04085, 04086, 04088–04091, 04099, 04101, 04106, 04109, 04320–04325); 1 isolated M₁ with sign of root-formation (YKS 00021); 21 isolated M₁ without sign of root-formation (YKS 04040, 04044, 04050, 04052, 04055, 04056, 04066–04068, 04073, 04074, 04293, 04326–04334); 14 isolated M₂ without sign of root-formation (YKS 04236, 04243, 04253, 04257, 04259, 04286, 04288, 04295, 04335–04340); 19 isolated M₃ without sign of root-formation (YKS 04120, 04121, 04127, 04129, 04135, 04136, 04142, 04143, 04272, 04290–04292, 04341–04347).

F₁, F₂ and F₄ of Kumaishi-do Cave

2 maxillae with M¹ (YKS 00287, 00304); 1 mandible with I, M₁ and M₂ (YKS 00300); 1 mandible with I and M₂ (YKS 00301); 1 mandible with M₁ (YKS 00071); 1 mandible with M₂ (YKS 00309); 1 mandible with I (YKS 00308); 1 mandible without teeth (YKS 00725); 67 isolated M¹ without sign of root-formation (YKS 00229, 00392, 00397–00399, 00430–00433, 00439, 00440, 00441, 00444, 00449, 00452, 00456, 00460, 00465, 00468–00474, 00476, 00478–00480, 00482–00484, 00487, 00488, 00492, 00495, 00497, 00499, 00501, 00503–00505, 00507–00509, 00511, 00514, 00516, 00517, 00519, 00521, 00523–00525, 00703, 00742, 00752, 00785, 00797, 00842, 00869, 00870, 00888, 00905, 00908–00910); 66 isolated M² without sign of root-formation (YKS 00698, 00700, 00701, 00704–00707, 00715, 00716,

00718–00721, 00724, 00732, 00733, 00735, 00740, 00743, 00753, 00757–00759, 00772, 00778–00782, 00784, 00786–00788, 00790, 00792, 00795, 00798, 00802, 00804, 00806, 00809, 00812, 00817, 00818, 00822, 00826, 00831, 00837–00839, 00841, 00844–00846, 00848, 00850, 00854, 00855, 00857, 00861, 00863–00865, 00867, 00875, 00889); 40 isolated M^3 without sign of root-formation (YKS 00165, 00176, 00177, 00183, 00185, 00187, 00193, 00194, 00197–00200, 00202, 00204, 00205, 00208–00210, 00212–00214, 00266–00272, 00274–00276, 00279, 00281, 00282, 00284, 00728, 00734, 00748, 00762, 00886); 87 isolated M_1 without sign of root-formation (YKS 00001, 00002, 00011, 00015–00020, 00024, 00025, 00029–00031, 00033, 00037, 00041, 00045–00047, 00050–00056, 00059–00062, 00067, 00068, 00070, 00073, 00075–00079, 00082, 00086, 00087, 00090–00104, 00106, 00110–00112, 00215–00223, 00722, 00745, 00747, 00770, 00794, 00799, 00801, 00808, 00814, 00825, 00828, 00871, 00895–00897, 00906); 1 isolated M_2 with roots (YKS 00823); 63 isolated M_2 without sign of root-formation (YKS 00527, 00534, 00539, 00540, 00543–00547, 00549, 00550, 00553, 00556, 00560, 00562–00564, 00566, 00567, 00569–00575, 00578–00589, 00591–00594, 00597–00601, 00604, 00605, 00608, 00611, 00613, 00744, 00746, 0783, 00815, 00843, 00862, 00872, 00876, 00891, 00915, 00916); 51 isolated M_3 without sign of root-formation (YKS 00614, 00615, 00617–00619, 00621, 00622, 00625, 00627, 00628, 00630, 00632, 00633, 00635, 00636, 00638–00640, 00644, 00645, 00647, 00649, 00650, 00653, 00655–00657, 00661, 00662, 00665, 00667–00674, 00676–00678, 00681, 0682, 00684, 00685, 00702, 00708, 00709, 00796, 00830, 00892).

Kumaishi-do Cave (site unknown; isolated molars without sign of root-formation)

3 M^1 (YKS 00429, 00445, 00446); 3 M^2 (YKS 00700, 00701, 00730); 1 M^3 (YKS 00175); 3 M_1 (YKS 00003, 00010, 00014); 4 M_2 (YKS 00537, 00538, 00556); 1 M_3 (YKS 00702).

Geological distribution — Late Pleistocene.

Geographical distribution — Hitherto known only from Honshu.

Description

The morphology of the maxilla and mandible is not different significantly from that of *Clethrionomys japonicus*, *Phaulomys* cf. *smithii* and the living species of *Phaulomys*. The basic patterns of the molars are also identical with those of these species (namely the general feature and number of the triangles, anterior loop and posterior loop as well as the number of the salient and re-entrant angles). However the detailed observation shows that the molars with roots or sign of root-formation have strong resemblance to the molars of *C. japonicus*, while the molars without sign of root-formation are very similar to those of *P. cf. smithii* from the Late Pleistocene localities. Therefore these two types of the molars are described independently. In the description of the former type, the result of the numerical analysis of the assemblage from Sugi-ana Cave is exclusively shown, because it is the only assemblage suitable for the analysis. In the description of the latter type, the results of all the localities are given in parenthesis, where the abbreviations such as S, F_3 and $F_{1,2,4}$ are used. They mean Sugi-ana Cave, F_3 of Kumaishi-do Cave, and F_1 , F_2 and F_4 of the same cave respectively. The detailed description of the molars is given below.

M¹ with roots or sign of root-formation (Pl. 1) —

The anterior wall of the anterior loop is always single-lobed. The anterolingual conule is usually larger than the anterolabial conule. Is 1, Is 3 and Is 4 are closed in most specimens (13 specimens out of 14), while Is 2 is closed in 12 specimens out of 14. The second minor fold is always recognized, but it is generally very weak. The second secondary fold is absent in 10 specimens out of 14. In other four specimens, it is weakly developed.

M¹ without sign of root-formation —

The anterior wall of the anterior loop is always single-lobed in both assemblages of Kumaishi-do Cave. In Sugi-ana Cave, it is single-lobed in 94.1% of 68 specimens, whereas the remaining specimens have bilobed or trilobed anterior loops (4.4% and 1.5% respectively). The anterolingual conule is larger than or as large as the anterolabial conule in almost all the specimens (generally more than 95%) as in *C. japonicus*. The isthmuses are usually closed (generally more than 75% in each isthmus). The frequency of their closing is somewhat higher than in *P. cf. smithii* from Tanuki-ana Cave, but nearly as high as in the same form from the Late Pleistocene horizons of Kannondo Cave Site (Table 51). The second minor fold is more or less developed in most specimens (98.5% of 66 specimens in S; 92.3% of 53 specimens in F_{1,2,4}). The second secondary fold is often unrecognized (67.6% of 68 specimens in S; 70.6% of 51 specimens in F_{1,2,4}). It is generally weak, when it is recognized.

*M*² with roots or sign of root-formation (Pl. 4) —

The anterior wall of the anterior loop is single-lobed in most specimens (8 specimens out of 9). The isthmuses are always closed. The second minor fold is usually recognized (in 8 specimens out of 10), while the second secondary fold is undeveloped in most specimens (9 specimens out of 10).

*M*² without sign of root-formation —

The anterior wall of the anterior loop is always single-lobed in the specimens from Sugi-ana Cave and F₃ of Kumaishi-do Cave. In the assemblage of F₁, F₂ and F₄ of Kumaishi-do Cave, it is single-lobed in 57 specimens out of 58, while the remaining one specimen has a bilobed anterior loop. The isthmuses are usually closed (generally more than 90%). The frequency of their closing is higher than that in *P. cf. smithii* from Tanuki-ana Cave, but nearly as high as the same form from the Late Pleistocene horizons of Kannondo Cave Site (Table 51). The second minor fold is always or usually recognized (100% of 56 specimens in S; also 100% of 18 specimens in F₃; 91.2% of 57 specimens in F_{1,2,4}). On the other hand, the second secondary fold is usually unrecognized (80.4% of 56 specimens in S; 77.8% of 18 specimens in F₃; 82.1% of 56 specimens in F_{1,2,4}).

*M*³ with roots or sign of root-formation (Pls. 6, 7) —

The anterior wall of the anterior loop is single-lobed in 10 specimens out of 14, while it is bilobed in the remaining specimens. Is 2 is always closed, while Is 3 is closed in 13 specimens out of 14. The frequency of the closing of Is 4 is somewhat lower (12 specimens out of 14). Is 5 is often open (in 7 specimens out of 13). The posterior loop is usually simple. The morphotype S is most frequently found (6 specimens out of 13), while L₁, L₂ and C₁ appear in two specimens each. The remaining one specimen belongs to the morphotype C₂.

*M*³ without sign of root-formation —

The anterior wall of the anterior loop is usually or often single-lobed (79.6% of 157 specimens in S; 60.0% of 20 specimens in F₃; 83.8% of 37 specimens in F_{1,2,4}). The remaining specimens are bilobed. Is 2 is almost always closed (more than 95%). The frequency of the closing of Is 3 is variable in each locality (ca. 80% in F₃; 10–30% in S and F_{1,2,4}). That of Is 5 is also variable (ca. 80% in F₃; ca. 60% in S; ca. 40% in F_{1,2,4}). Is 4 is usually or often closed (90–60%). As regards the shape of the posterior loop, the complicate morphotypes such as C₁

Table 44. Number of the specimens belonging to each morphotype in M^3 of *Phaulomys* cf. *smithii* and *Clethrionomys-Phaulomys* transitional form.
 * SOTSUKA Collection; rooted $M^3=M^3$ with roots or sign of root-formation;
 unrooted $M^3=M^3$ without sign of root-formation.

LOCALITY	MORPHOTYPE								TOTAL
	S	L ₁	L ₂	C ₁	C ₂	F ₁	F ₂	Ab	

<i>Phaulomys</i> cf. <i>smithii</i>									
Yakubono-ana Cave*	—	—	—	—	1	—	—	—	1
Oiwa-ana Cave*	—	—	—	—	1	—	—	—	1
Ninjinkubo First Cave*	1	1	1	—	—	—	—	—	3
Husen-ana Cave	1	3	5	3	11	—	1	—	24
Tanuki-ana Cave									
Layer 1	—	—	3	1	8	—	—	—	12
Layer 2	1	13	20	9	21	1	—	—	65
Layers 2 to 3	—	—	—	2	2	—	—	—	4
Layer 3	—	1	1	1	5	—	—	—	8
Layer 4	3	7	10	3	18	—	1	—	42
Domen Cave Site									
Horizon unknown	—	—	—	—	1	—	—	—	1
Horizon V	—	2	2	1	1	—	—	2	8
Kannondo Cave Site									
Horizon M (upper)	1	1	2	2	9	—	—	—	15
Horizon M (lower)	—	1	1	2	2	—	—	—	6
Horizon N	—	2	3	2	—	—	—	1	8
Horizon O (upper)	5	14	13	8	6	—	—	—	46
Horizon O (lower)	—	1	3	2	3	—	—	—	9
Horizon P	1	—	3	—	1	—	—	—	5
Yage Quarry									
Site 4	—	1	—	—	—	—	—	—	1

<i>Clethrionomys</i> — <i>Phaulomys</i> transitional form									
Kumaishi-do Cave (unrooted M ³)									
F ₁ , F ₂ and F ₄	5	7	3	7	10	—	—	1	33
F ₃	2	1	1	7	8	—	—	—	19
Sugi-ana Cave									
Rooted M ³	6	2	2	2	1	—	—	—	13
Unrooted M ³	13	15	30	29	79	—	2	5	173

and C₂ are predominantly found, while the frequency of the morphotype S is considerably low (Table 44; Fig. 114). The frequency distribution of each morphotype is rather similar to that of *P.* cf. *smithii* than that of *C. japonicus*.

*M*₁ with roots or sign of root-formation (Pls. 9–11) —

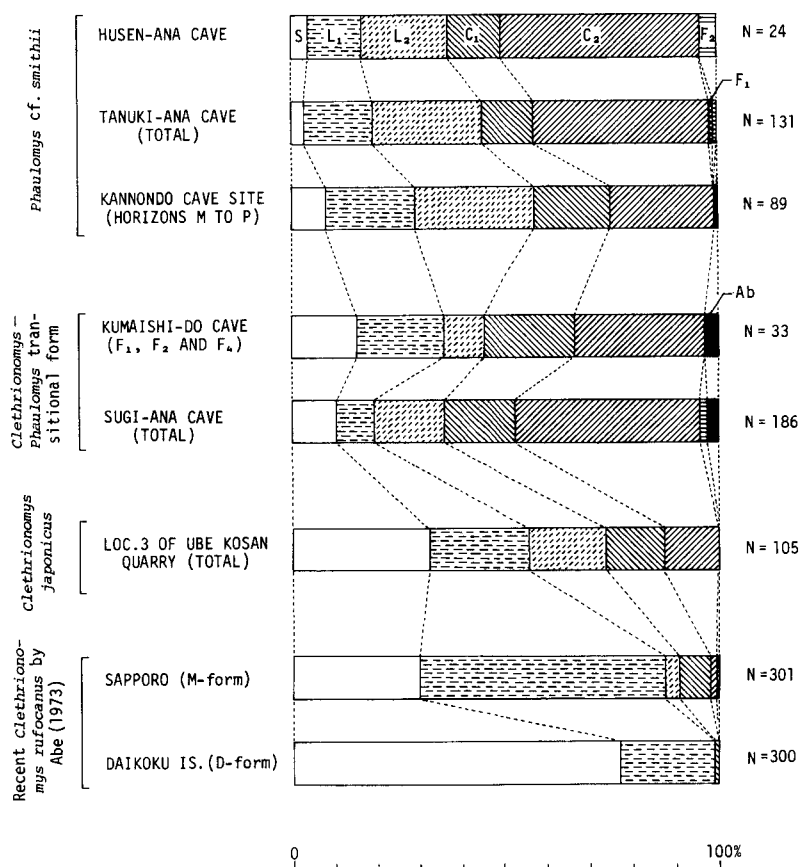


Fig. 114. Frequency of appearance of each morphotype in M^3 of *Clethrionomys japonicus*, sp. nov., *Clethrionomys-Phaulomys* transitional form, *Phaulomys cf. smithii* and the recent *C. rufocanus*. N, number of examined specimens.

As regards the variation of the anterior loop, the morphotypes 1 and 2 are predominantly found in younger age-classes (II-I to III), but they become few in older age-classes, where the morphotypes 3 and 4 predominate. The anterior wall of the anterior loop is always single-lobed. The anterolabial conulid is usually larger than the anterolingual conulid. Is 6 and Is 5 are usually open, while Is 4, Is 3 and Is 1 are always closed (Table 45). The frequency of the closing of Is 2 is somewhat lower than those of the last three isthmuses. When Is 2 is open, its width is not broad. In one specimen from Sugi-ana Cave, a small closed enamel ring is observed at Is 1 (7 of Pl. 11), but such a ring is never found in other specimens. The posterior wall of the posterior loop is always single-lobed.

M₁ without sign of root-formation (Pls. 16, 17) —

The molar pattern is more variable than in *C. japonicus*. As regards the morphology of the anterior loop, the morphotype 2 is most frequently found in Sugi-ana Cave and F₁, F₂, F₄ of

Table 45. Frequency of closing of each isthmus in M_1 of *Clethrionomys-Phaulomys* transitional form. The number in parenthesis indicates the total number of the examined specimens.

ISTHMUS	M_1 with roots or sign of root-formation	M_1 without sign of root-formation		
		SUGI-ANA CAVE	F_3 OF KUMA- ISHI-DO CAVE	F_1, F_2 AND F_4 OF KUMAISHI-DO CAVE
Is 6	10.0% (20)	9.4% (85)	10.0% (20)	14.3% (42)
Is 5	20.0 (20)	18.6 (87)	19.0 (21)	23.3 (43)
Is 4	100.0 (20)	30.7 (88)	90.5 (21)	38.6 (44)
Is 3	100.0 (20)	90.1 (87)	95.2 (21)	90.9 (44)
Is 2	85.0 (20)	14.3 (84)	66.7 (21)	22.7 (44)
Is 1	100.0 (20)	100.0 (84)	100.0 (21)	97.7 (44)

Table 46. Number of the specimens belonging to each morphotype in M_1 of *Clethrionomys-Phaulomys* transitional form and *Phaulomys* cf. *smithii*.
* M_1 without sign of root-formation.

LOCALITY	MORPHOTYPE				TOTAL
	1	2	3	4	
<i>Phaulomys</i> cf. <i>smithii</i>					
Husen-ana Cave	3	13	13	2	31
Kannondo Cave Site					
Horizon M (upper)	8	12	6	2	28
Horizon O (upper)	13	16	12	4	45
<i>Clethrionomys</i> - <i>Phaulomys</i> transitional form					
Kumaishi-do Cave*					
F ₁ , F ₂ and F ₄	22	34	16	16	88
F ₃	7	4	1	1	13
Sugi-ana Cave*	24	38	20	10	92

Kumaishi-do Cave (Table 46; Fig. 115). The frequencies of the morphotypes 1 and 3 are considerably lower, and that of 4 is lowest in these localities. On the other hand, the morphotype 1 occurs most frequently in F_3 of Kumaishi-do Cave. The anterior wall of the

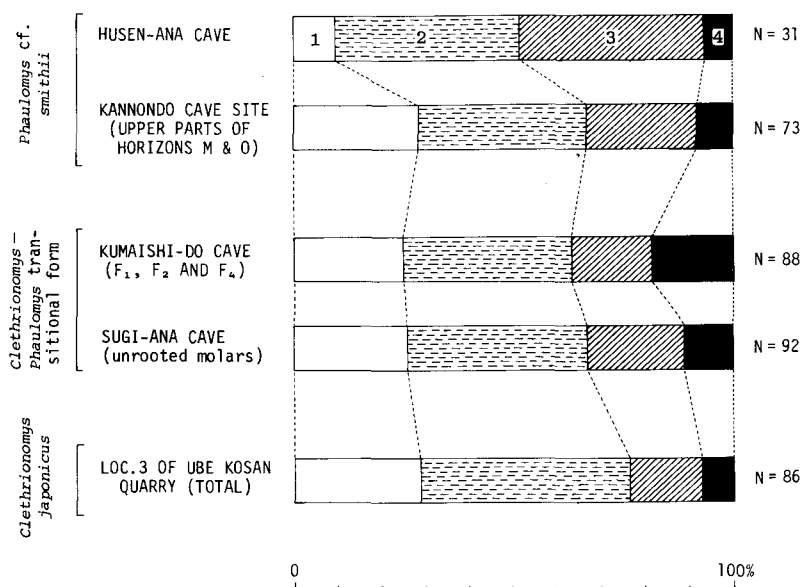


Fig. 115. Frequency of appearance of each morphotype in M_1 of *Clethrionomys japonicus*, sp. nov., *Clethrionomys-Phaulomys* transitional form and *Phaulomys* cf. *smithii*. N, number of examined specimens.

anterior loop is almost always single-lobed. In young individuals, however, it is sometimes bilobed or trilobed. The anterolabial conulid is usually as large as or larger than the anterolingual conulids. The triangles are somewhat less alternating than in the specimens with roots or sign of root-formation. The isthmuses are generally more frequently open than in the same specimens (Pls. 9–11, 16, 17, Table 45). Namely Is 6 and Is 5 are usually open, while Is 3 is usually closed. The frequencies of the closing of Is 4 and Is 2 are variable in each locality. They are much higher in F_3 of Kumaishi-do Cave than in Sugi-ana Cave and in F_1 , F_2 and F_4 of Kumaishi-do Cave. On the other hand, Is 1 is almost always closed. The posterior wall of the posterior loop is single-lobed in most specimens (94.1% of 102 specimens in S; 95.2% of 21 specimens in F_3 ; 94.9% in 39 specimens in $F_{1,2,4}$).

M₂ with roots or sign of root-formation (Pl. 12) —

The first secondary fold is recognized only in one specimen (YKS 00823 from F_4 of Kumaishi-do Cave). The anterior labial fold is always absent. Each triangle is well alternating. Is 4 is always open, while Is 3 and Is 1 are always closed. Is 2 is closed in two specimens out of six. The posterior wall of the posterior loop is always single-lobed.

M₂ without sign of root-formation —

The first secondary fold is often or usually recognized (61.8% of 102 specimens in S; 75.0% of 16 specimens in F_3 ; 52.8% of 55 specimens in $F_{1,2,4}$). When it is recognized, its concavity is generally weak. The anterior labial fold is always or usually absent (95.1% of 102 specimens in S; 100% of 16 specimens in F_3 ; 85.7% of 56 specimens in $F_{1,2,4}$). In some young

individuals, however, this fold is strongly developed. Each triangle is less alternating in the assemblages of Sugi-ana Cave and of F_1 , F_2 , and F_4 of Kumaishi-do Cave than in the specimens with roots or sign of root-formation. In F_3 of Kumaishi-do Cave, however, it is well alternating as in the latter specimens. Is 4 is almost always open (more than 97%), while Is 3 and Is 1 are almost always closed (more than 96%). Is 2 is usually open in Sugi-ana Cave, and F_1 , F_2 and F_4 of Kumaishi-do Cave (92.9% of 98 specimens and 94.2% of 52 specimens respectively). In F_3 of Kumaishi-do Cave, however, it is often closed (68.8% of 16 specimens). The posterior wall of the posterior loop is always single-lobed.

M₃ with roots or sign of root-formation (Pl. 14) —

The first secondary fold is often recognized, but its concavity is slight. The anterior labial fold is always absent. Is 4 and Is 2 are always broadly open, while Is 1 and Is 3 are always closed. The posterior wall of the posterior loop is always single-lobed.

M₃ without sign of root-formation —

The first secondary fold is usually or often lacking (79.3% of 82 specimens in S; 70.0% of 20 specimens in F_3 ; 85.1% of 47 specimens in $F_{1,2,4}$). When this fold is recognized, its concavity is slight. The anterior labial fold is almost always or usually absent (90.1% of 81 specimens in S; 95.0% of 20 specimens in F_3 ; 93.6% of 47 specimens in $F_{1,2,4}$). Is 4 is always open, while Is 3 and Is 1 are almost always closed (more than 95%). Is 2 is always open in Sugi-ana Cave and in F_1 , F_2 and F_4 of Kumaishi-do Cave. In F_3 of the latter cave, however, it is sometimes closed (10.5% of 19 specimens). The posterior wall of the posterior loop is almost always single-lobed. However it is rarely bilobed (2.5% of 80 specimens in S; 7.1% of 42 specimens in $F_{1,2,4}$).

Two specimens from Sugi-ana Cave have very unusual patterns (5 and 6 of Fig. 116). In one specimen (KUJC99840), a distinct swelling is observed on the posterior enamel wall of T1. In another specimen (KUJC99841), the buccal re-entrant angles are very shallow, and almost unrecognized. Such characters of these specimens are never observed in other specimens.

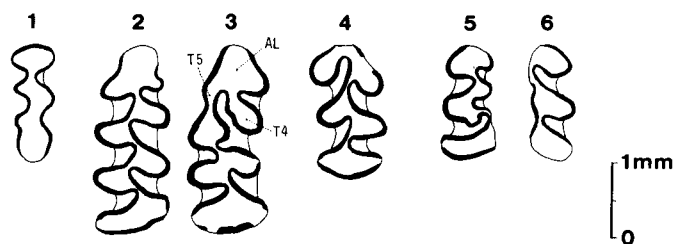


Fig. 116. *Clethrionomys-Phaulomys* transitional form and *Phaulomys* cf. *smithii*. Molars with unusual patterns are shown. AL, anterior loop.

1-4, *P. cf. smithii* from the Late Pleistocene horizons of Kannondo Cave Site. 1, right M^3 from Horizon P (HUA-K00710); 2, right M_1 from Horizon N (HUA-K01210); 3, right M_1 from the upper part of Horizon O (HUA-K00936); 4, left M_2 from Horizon P (HUA-K00730).

5-6, *Clethrionomys-Phaulomys* transitional form from Sugi-ana Cave. 5, right M_3 (KUJC99840); 6, left M_3 (KUJC99841).

Measurements

The measurements of the mandibles and molars are given in Tables 47 and 48 respectively. The latter table shows that the molars with roots or sign of root-formation are considerably larger than those without sign of root-formation. This size difference can be interpreted as depending on the ontogenetic size change of the occlusal surfaces of the molars as observed in *C. japonicus* (p. 229 and Fig. 112).

Discussion

Among the species of *Clethrionomys*, *C. japonicus* has great resemblance to the species assigned to *Phaulomys* in the present paper (the recent *P. andersoni* and *P. smithii*, and the fossils closely related to these species). The reasons for the generic allocation of these species to *Phaulomys* are discussed in the subsequent section (p. 255). The main differences between *C. japonicus* and the species of *Phaulomys* are summarized as follows:

1. The molars are rooted in *C. japonicus*, while they remain unrooted throughout life in the species of *Phaulomys*.
2. The isthmuses tend to be closed in *C. japonicus*, while some of them tend to be open in the species of *Phaulomys*.
3. The frequency of appearance of the complicate morphotypes of M^3 is lower in *C. japonicus* than in the species of *Phaulomys*.

The specimens from Sugi-ana Cave and Kumaishi-do Cave described here have intermediate characters between *C. japonicus* and the species of *Phaulomys*. Namely the specimens with roots or sign of root-formation are rarely found in the assemblages of these localities. The frequency of appearance of these specimens is much lower than in *C. japonicus*, but higher than in the species of *Phaulomys* where these specimens are completely absent (Fig. 117). This fact indicates that the molars from Sugi-ana Cave and Kumaishi-do Cave became rooted much later in life than those of *C. japonicus*. The isthmuses of the molars with roots or sign of root-formation from these localities are closed in similar frequencies to those of *C. japonicus*. On the other hand, the molars without sign of root-formation from the same localities are near to those of *Phaulomys* from the Late Pleistocene localities and the recent *P. andersoni* in this character. As regards the frequency of appearance of the complicate morphotypes of M^3 , the same tendency is generally observable (Tables 34, 44; Fig. 114). Therefore the specimens from Sugi-ana Cave and Kumaishi-do Cave can be considered to belong to an intermediate form which links *C. japonicus* with the species of *Phaulomys*. It is the reason why these specimens are referred to "*Clethrionomys-Phaulomys* transitional form" here.

In the lineage from *C. japonicus* to *Phaulomys*, the time of root-formation was gradually delayed with geological age. This tendency is already observed in the populations of *C. japonicus* as mentioned in the section of "age structure of fossil assemblage" of this species (p. 227). During the Late Pleistocene, the time of root-formation became much later in life, and finally the molars became unrooted throughout life as seen in the species of *Phaulomys*. In association with this change, some isthmuses became open, and the complexity of the posterior loop of M^3 increased.

The two recent species of *Phaulomys* are very similar to each other in osteological and dental

Table 47. Measurements of the mandibles of *Clethrionomys-Phaulomys* transitional form in mm. The numbers on the left side correspond to those in Fig. 72.

	Kumaishi-do Cave					S u g i - a n a C a v e					
	F ₁ , F ₂ and F ₄			F ₃							
	YKS 00300	YKS 00308	YKS 04001	YKS 04006	YKS 04021	KUJC 98199	KUJC 98176	KUJC 98185	KUJC 98176	KUJC 98161	KUJC 98192
2. Total length of the mandible (id to the condyle)	—	—	—	—	—	—	—	—	14.12	—	—
4. Length of the horizontal ramus	—	—	—	—	—	—	—	—	8.58	—	—
5. Length of the diastema	—	—	3.94	—	—	—	—	—	3.28	—	—
6. Length of the ascending ramus (the posterior border of M ₃ to the condyle)	—	—	—	—	—	6.31±	6.29±	—	6.25	—	—
8. Height of the ascending ramus (gov to the highest point of the condyle)	—	—	—	—	—	—	—	—	6.94	—	—
10. Ditto (gov to the mandibular incision)	—	—	—	—	—	—	—	—	5.41	—	—
12. Maximum height of the horizontal ramus	3.08	2.77	3.32	3.56	3.14	—	3.12	3.04	3.09	2.87	2.43
14. Maximum thickness of the horizontal ramus	2.19	2.24	2.47	2.72	2.51	—	2.35	2.48	2.32	2.23	1.90
16. Length of the molar row (M ₁ to M ₃) at the alveoli	—	—	—	—	—	5.65±	5.50±	5.72	5.47	—	—
17. Length of the molar row (M ₁ to M ₂) at the crowns	3.67	—	4.06	—	—	—	3.80	—	3.50	3.60	—
18. Ditto at the alveoli	3.95±	3.63±	4.17±	4.33±	4.23±	3.88	3.68±	3.65±	3.77±	3.76	3.69

Table 48. Measurements of the molars of *Clethrionomys-Phaulomys* transitional form in mm. For the distinction between "rooted" and "unrooted" molars see the caption of Table 44. Abbreviations as in Table 38.

TOOTH KIND AND LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
M¹										
Kumaishi-do Cave										
Locality unknown (unrooted M ¹)	1	—	1.69	—	—	2	0.95	1.06	1.16	—
F ₁ , F ₂ and F ₄ (unrooted M ¹)	48	1.62	1.94	2.25	0.12	44	0.94	1.06	1.24	0.07
F ₃ (unrooted M ¹)	4	1.88	2.12	2.31	—	4	1.07	1.13	1.18	—
Sugi-ana Cave										
Rooted M ¹	12	1.99	2.17	2.40	0.14	14	0.93	1.17	1.36	0.11
Unrooted M ¹	10	1.76	1.92	2.17	0.13	9	0.97	1.03	1.15	0.05
M²										
Kumaishi-do Cave										
Locality unknown (unrooted M ²)	2	1.35	1.37	1.39	—	2	0.90	0.90	0.90	—
F ₁ , F ₂ and F ₄ (unrooted M ²)	12	1.30	1.42	1.59	0.10	12	0.80	0.91	1.01	0.07
F ₃ (unrooted M ²)	6	1.47	1.58	1.65	0.07	8	0.80	0.97	1.19	0.10
Sugi-ana Cave										
Rooted M ²	9	1.47	1.64	1.84	0.12	10	0.91	1.04	1.19	0.07
Unrooted M ²	9	1.30	1.45	1.57	0.08	10	0.73	0.90	0.99	0.07
M³										
Kumaishi-do Cave										
F ₁ , F ₂ and F ₄ (unrooted M ³)	18	1.49	1.69	1.99	0.12	21	0.73	0.83	0.92	0.06
F ₃ (unrooted M ³)	13	1.66	1.91	2.08	0.12	13	0.76	0.88	1.03	0.08
Sugi-ana Cave										
Rooted M ³	12	1.64	1.89	2.31	0.18	14	0.84	0.94	1.23	0.10
Unrooted M ³	12	1.45	1.70	1.84	0.11	12	0.63	0.78	0.88	0.07
M₁										
Kumaishi-do Cave										
Locality unknown (unrooted M ₁)	3	2.19	2.29	2.42	—	3	0.94	0.99	1.04	—
F ₁ , F ₂ and F ₄ (unrooted M ₁)	65	1.80	2.17	2.51	0.14	70	0.73	0.94	1.15	0.07
F ₃										
Rooted M ₁	1	—	2.42	—	—	1	—	1.15	—	—
Unrooted M ₁	12	2.31	2.48	2.59	0.08	13	0.96	1.08	1.18	0.06
Sugi-ana Cave										
Rooted M ₁	19	2.32	2.57	2.82	0.15	20	0.97	1.13	1.26	0.09
Unrooted M ₁	85	1.81	2.21	2.60	0.13	98	0.74	0.94	1.09	0.07
M₂										
Kumaishi-do Cave										
Locality unknown (unrooted M ₂)	4	1.30	1.44	1.54	—	4	0.80	0.85	0.95	—
F ₁ , F ₂ and F ₄										
Rooted M ₂	1	—	1.78	—	—	1	—	0.85	—	—
Unrooted M ₂	51	1.20	1.41	1.59	0.09	53	0.68	0.83	0.95	0.07
F ₃ (unrooted M ₂)	10	1.47	1.61	1.75	0.08	10	0.88	0.96	1.03	0.05
Sugi-ana Cave										
Rooted M ₂	5	1.56	1.66	1.84	0.10	5	0.93	1.00	1.09	0.06
Unrooted M ₂	5	1.26	1.42	1.64	0.12	6	0.81	0.88	0.94	0.04
M₃										
Kumaishi-do Cave										
F ₁ , F ₂ and F ₄ (unrooted M ₃)	40	1.10	1.41	1.70	0.14	43	0.46	0.69	0.84	0.07
F ₃ (unrooted M ₃)	12	1.54	1.67	1.98	0.12	13	0.70	0.80	0.87	0.04
Sugi-ana Cave										
Rooted M ₃	9	1.43	1.63	1.98	0.16	9	0.72	0.80	0.94	0.06
Unrooted M ₃	6	1.31	1.47	1.62	0.11	8	0.57	0.70	0.75	0.06

characters. The differences between them are observed only in size and the frequency of closing of each isthmus. Namely, *P. andersoni* is slightly larger than *P. smithii*, although the ranges of the size variation are partly overlapped with each other. In addition, the frequencies of closing of the isthmuses are somewhat higher in *P. andersoni* than in *P. smithii* (especially in Is 3 and Is 5 of M^3 , Is 2 and Is 4 of M_1 , and Is 2 of M_2). Taking these differences into consideration, the fossil assemblage from F_3 of Kumaishi-do Cave is rather near to *P. andersoni*, while that from F_1 , F_2 and F_4 of the same locality rather approaches *P. smithii* (Tables 45, 48, 51, 52, 54–59). Therefore the assemblage from F_3 might be the ancestor of *P. andersoni*, while that from F_1 , F_2 and F_4 might belong to the lineage to *P. smithii*. The phylogenetic relationship

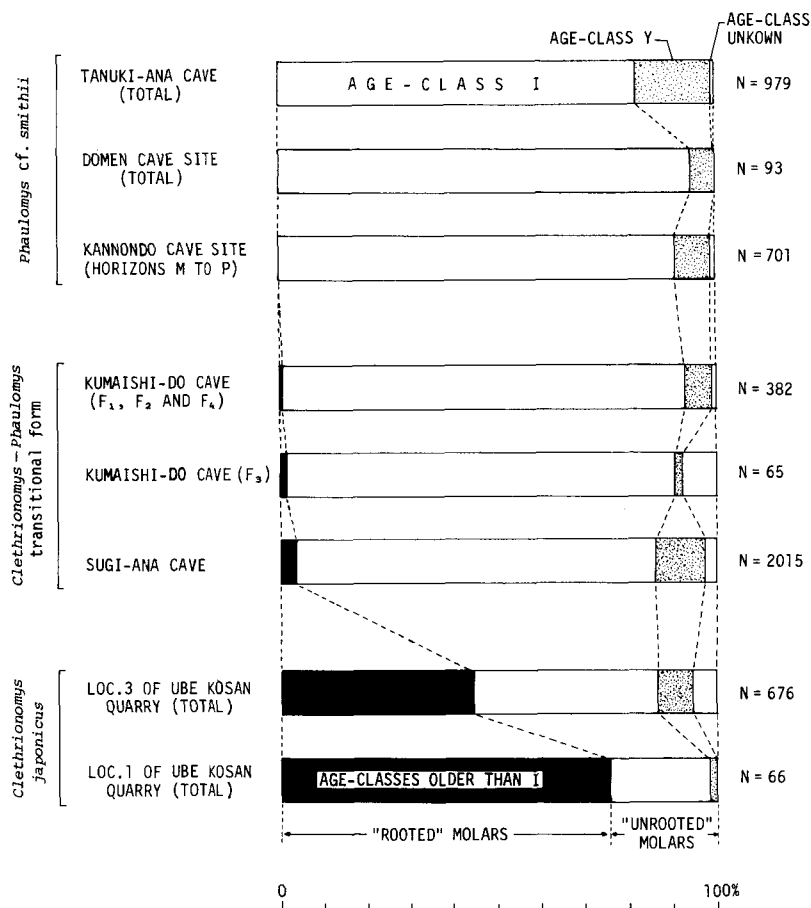


Fig. 117. Ratio of the molars with roots or sign of root-formation ("rooted molars"=molars belonging to the age-classes older than I) and those without sign of root-formation ("unrooted molars"=molars belonging to the age-classes I and Y) against the total number of the examined specimens (N) in the assemblages of *Clethrionomys japonicus*, sp. nov., *Clethrionomys-Phaulomys* transitional form and *Phaulomys cf. smithii*. All kinds of molar are put together.

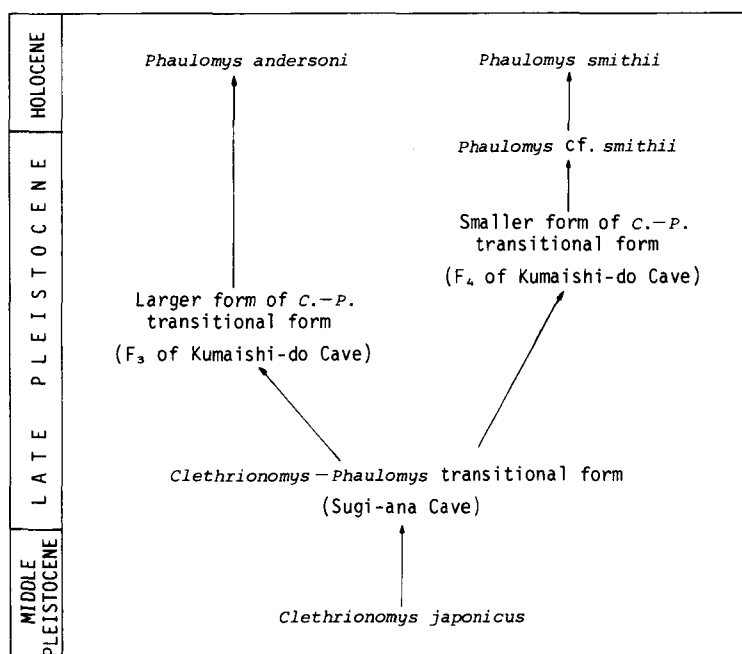


Fig. 118. Proposed phylogenetic relationship among *Clethrionomys japonicus*, *Clethrionomys-Phaulomys* transitional form, *Phaulomys smithii* and *P. andersoni*.

among *C. japonicus*, *Clethrionomys-Phaulomys* transitional form and the species of *Phaulomys* proposed here is shown in Fig. 118.

Genus *Phaulomys* THOMAS, 1905

Type species — *P. smithii* (THOMAS, 1905).

Included species — *P. smithii* and *P. andersoni* (THOMAS, 1905).

Characters

The interorbital region is flattened without the interorbital crest seen in *Hyperacrius*. The bony palate terminates posteriorly in simple structure as in *Clethrionomys*. The area between the alveoli of the lower molars and the ascending ramus is flattened or slightly concave. The capsule for the lower incisor on the lingual face of the ascending ramus is weak. The posterior end of the lower incisor is nearly as high as the level of the occlusal surfaces of the lower molars, but lower than the mandibular foramen.

The molars remain unrooted throughout life. The salient angles are generally blunter than in *Clethrionomys*. The re-entrant angles are narrower than in *Alticola* and *Hyperacrius*, but as broad as in *Clethrionomys* and *Eothenomys*. They are filled with rich cementum. The enamel

band becomes somewhat thinner at the bottom of each re-entrant angle, but the differentiation of its thickness is not so remarkable as in *Microtus*. In each triangle, the enamel band on the concave side has nearly the same thickness as that on the convex side. The isthmuses are generally more frequently open than in *Clethrionomys* (especially Is 3 of M^3 and Is 2 of M_1). M^1 and M^2 always lack the additional postero-lingual angle (LSA4). T1 and T3 of M^1 and T3 of M^2 are not so elongated as in *Microtus*. In M^3 , three or four salient angles are observed on each side. LSA6 and LRA5 are always absent. BRA1 is always deep, and Is 2 is closed or narrow so that the anterior loop is well separated from T2. The posterior loop of M^3 is variable in complexity. The anterior loop of M_1 is elliptical or half-oval, and sometimes confluent with T5. Therefore LSA5 and BSA4 are blunter and give different appearance from other salient angles. In this molar, LRA4 is shallower than other lingual re-entrant angles, and LRA5 is always absent. BRA4 is also almost always absent. In M_3 , BSA3 is well developed. The confluence of dentine field is observed between T1 and T2 as well as between T3 and T4 as in *Clethrionomys*.

Discussion

Several previous authors have argued the generic allocation of the red-backed voles distributed in the present Honshu, Shikoku, Kyushu and Oki Islands. THOMAS (1905a, b) described these voles as two new species of *Evotomys* (= *Clethrionomys*), *E. smithii* and *E. andersoni*. In 1909, ANDERSON added a different new species, *niigatae*. This species was placed in *Craseomys* which is now synonymized with *Clethrionomys*. The allocation of these species to *Clethrionomys* were accepted by AOKI (1915), KISHIDA (1924), WATANABE (1937), HANAOKA (1937a, b), KURODA (1940) and TOKUDA (1941b). On the other hand, HINTON (1926) and ELLERMAN and MORRISON-SCOTT (1951) also placed them in *Clethrionomys*, although they considered *andersoni* and *niigatae* as synonyms of *smithii* which was treated only as a subspecies of *C. rufocanus*. Subsequent authors such as IMAIZUMI (1949) and KURODA (1953) transferred *smithii* to *Eothenomys*, but left *andersoni* as a subspecies of *C. rufocanus*. In 1955, TOKUDA allocated *smithii* to *Antelionomys* which is now generally included in *Eothenomys*. In 1957, IMAIZUMI proposed a new species, *kageus*, and allocated it to *Eothenomys* as well as *smithii*. In his monograph of 1960, IMAIZUMI followed his paper of 1957 on the generic allocation of *smithii* and *kageus*, but regarded *andersoni* and *niigatae* as independent species of *Aschizomys*. JAMESON (1961) followed this opinion, excepting the treatment of *Aschizomys*. He considered it as a subgenus of *Clethrionomys* and added a new species, *imaizumii* to this subgenus. Subsequently TANAKA (1971) gave a generic rank to *Phaulomys* which had been originally proposed as a subgenus of *Clethrionomys* by THOMAS (1905a). For *andersoni* and *niigatae*, TANAKA adopted *Craseomys* as a subgenus of *Clethrionomys* instead of *Aschizomys*. Recently CORBET (1978) synonymized *okiensis* and *kageus* with *smithii*, and *niigatae* and *imaizumii* with *andersoni* respectively. Moreover he allocated *smithii* to *Eothenomys*, but *andersoni* to *Clethrionomys*. AIMI's revision of these voles (1980) was coincident with this opinion except the generic allocation of *andersoni*. He concluded that *andersoni* should be placed in *Eothenomys* as well as *smithii*. AIMI's conclusion was followed by HONACKI *et al.* (1982).

Because the conclusions of CORBET (1978) and AIMI (1980) are considered to have good grounds in specific level, they are accepted here. Namely these red-backed voles are referable to the only two species, *smithii* and *andersoni*. The present author believes that these species are closely related with each other and should be allocated to a single genus, because they are quite similar to each other in osteological and dental characters. The palaeontological evidences provided in this paper indicate that these species did not migrate from the continent but evolved in Japan from the common ancestor, *Clethrionomys japonicus*. This lineage is independent from those of *Eothenomys*, *Alticola* and *Hyperacrius*, although these genera seem to be derived from the *Clethrionomys* stock (Fig. 113). Because it is generally accepted that rooted molars are diagnostic for the genus *Clethrionomys*, the allocation of *smithii* and *andersoni* to this genus is impossible. Therefore these species should be allocated to a distinct genus from *Clethrionomys*, *Eothenomys*, *Alticola* and *Hyperacrius*. As the name of this genus, the usage of *Phaulomys* is most reasonable.

Arvicolids are considered to have undergone rapid evolution during the Quaternary. Among the genera of this group, the lineage from *Mimomys* to *Arvicola* has been well investigated (HINTON, 1926; CHALINE, 1974a; CHALINE and MEIN, 1979; STUART, 1982). In this lineage, the first appearance of *Arvicola* is considered to be the later part of the Middle Pleistocene (ca. 0.3 million years B.P.; according to Fig. 11.3 of STUART, 1982). On the other hand, the present fossil evidences show that *Phaulomys* first appeared in the Late Pleistocene (possibly later than 0.1 million years B.P.). Therefore it can be said that *Phaulomys* arose more recently than *Arvicola*. Because the first appearances of other arvicolid genera are generally earlier than that of *Arvicola*, *Phaulomys* can be regarded as one of the most recently established genera among the arvicolids. The above-mentioned confusion on the classification and generic allocation of the recent species of this genus might be caused by the immaturity of each species owing to the shortage of time and by the parallel evolution to other groups (for example, some species of *Eothenomys*).

Because the fossils of *Phaulomys* abundantly occur in the Late Pleistocene and Holocene sediments of Honshu, Shikoku and Kyushu (Figs. 119, 120; Tables 49, 50), this genus has flourished in these periods. As seen in the present day, it has been well adapted to the temperate forests of these areas. The absence of *Phaulomys* from the present Hokkaido, Sado Island and Tsushima Island can be interpreted as depending on the lack of the land connection between Honshu (or Kyushu) and these islands during the Late Pleistocene.

Phaulomys cf. *smithii* (THOMAS, 1905)

(Figs. 116, 121, 122–124; Pls. 18, 19)

Materials —

Because the number of specimens is inadequate in Yage Quarry, Suse Quarry (East Fissure), Mejiro-do Cave, Anagami Rockshelter Site, Yoshigatani Third Cave, Ojika-do Cave and Yakubono-ana Cave, the identification of the materials from these localities is tentative.

LATE PLEISTOCENE LOCALITIES

Yage Quarry (Site 4)

1 isolated M³ (KUJC100040); 1 isolated M₃ (KUJC100041).

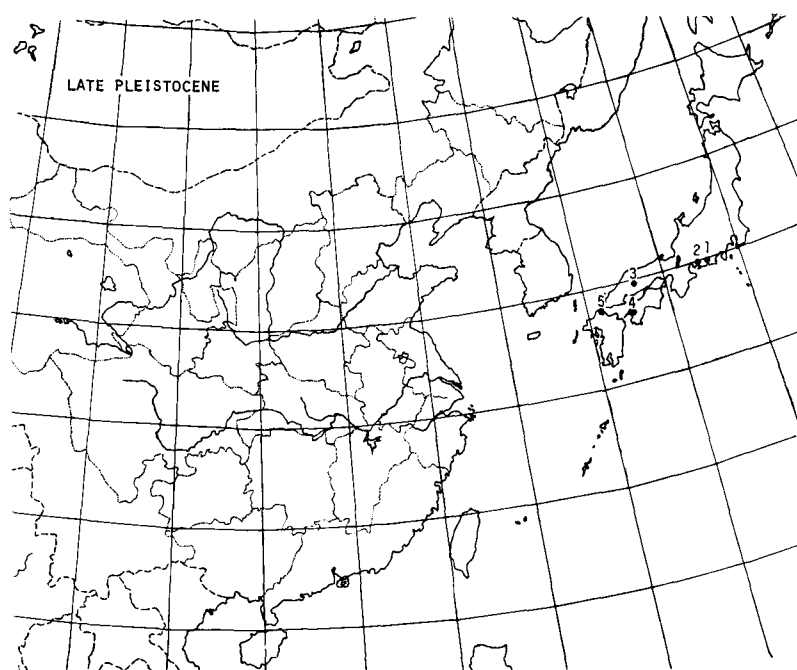


Fig. 119. Late Pleistocene fossil localities of *Phaulomys*. 1, Yage Quarry; 2, Suse Quarry; 3, Kannondo Cave Site; 4, Shikimizu Quarry; 5, Seiryukutsu Cave and Mejiro-do Cave. For detailed explanation see Table 49.

Table 49. Late Pleistocene fossil localities of *Phaulomys* (restricted to Japan). The numbers on the left side correspond to those in Fig. 119.

LOCALITY	REVISED IDENTIFICATION	REFERENCES	REMARKS
1. Yage Quarry (Site 4)	? <i>Phaulomys</i> cf. <i>smithii</i>	This paper	
2. Suse Quarry (East Fissure)	? <i>Phaulomys</i> cf. <i>smithii</i>	This paper	
3. Kannondo Cave Site	<i>Phaulomys</i> cf. <i>smithii</i>	Kawamura (1981, 1982); Kawamura et al. (1986); this paper	In the previous papers, it is identified as <i>Eothenomys</i> sp.
4. Shikimizu Quarry	? <i>Phaulomys</i> cf. <i>smithii</i>	Shikama & Hasegawa (1962); Hasegawa (1966); Kowalski & Hasegawa (1976)	In the previous papers, it is identified as <i>Clethrionomys</i> sp. or <i>Eothenomys smithii</i> .
5. Seiryukutsu Cave	<i>Phaulomys</i> cf. <i>smithii</i>	Kawamura & Sotsuka (1984); this paper	In the previous paper, it is identified as <i>Eothenomys</i> sp.
5. Mejiro-do Cave	? <i>Phaulomys</i> cf. <i>smithii</i>	Ditto	Ditto

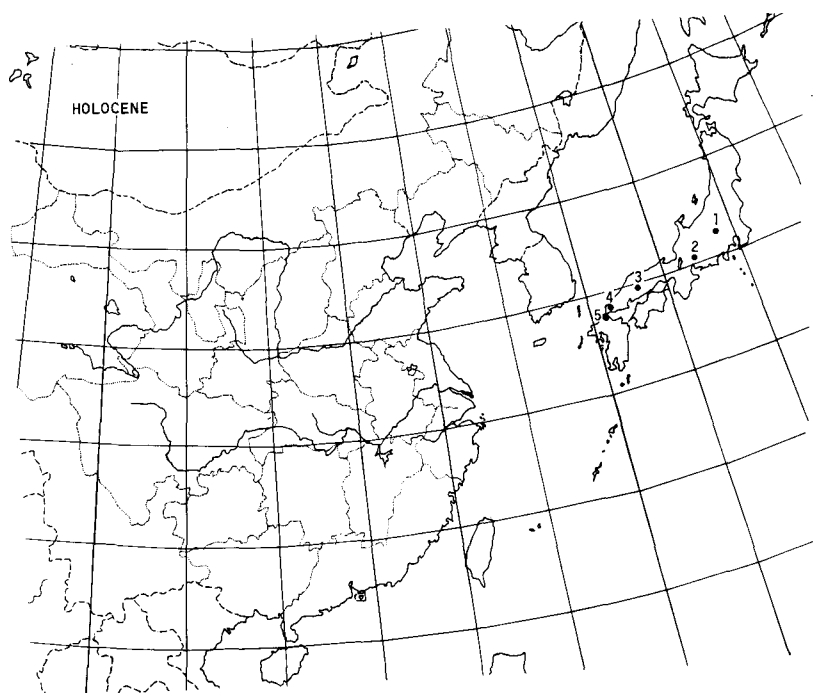


Fig. 120. Holocene fossil localities of *Phaulomys*. 1, Tochibara Rockshelter Site; 2, Miwa Cave; 3, Taishaku Area (Kannondo Cave Site, Anagami Rockshelter Site and Domen Cave Site); 4, Akiyoshi Area (Tanuki-ana Cave, Husen-ana Cave and Makurazino-ana Cave); 5, Hirao-dai Area (Ninjinkubo First Cave, Yakubono-ana Cave, Ojika-do Cave, Yoshigatani Third Cave and Oiwa-ana Cave). For detailed explanation see Table 50.

Seiryukutsu Cave (specimen numbers are prefixed by KMNH)

4 isolated M^1 (VP 300,007–300,010); 2 isolated M^2 (VP 300,011, 300,012); 1 mandible with M_1 and M_2 (VP 300,013); 1 mandible with M_1 (VP 300,014); 1 mandible with I (VP 300,015); 1 mandible without teeth (VP 300,016); 3 isolated M_1 (VP 300,017–300,019).

Kannondo Cave Site (specimen numbers are prefixed by HUA)

Horizon P: 6 isolated M^1 (K00690–00695); 14 isolated M^2 (K00696–00709); 7 isolated M^3 (K00710–00716); 1 mandible with M_1 and M_2 (K00717); 1 mandible without teeth (K00718); 11 isolated M_1 (K00719–00729); 7 isolated M_2 (K00730–00736); 4 isolated M_3 (K00737–00740).

Horizon O (lower part): 18 isolated M^1 (K00741–00758); 12 isolated M^2 (K00759–00770); 12 isolated M^3 (K00771–00782); 1 mandible with I, M_1 and M_2 (K00783); 1 mandible with M_1 and M_2 (K00784); 1 mandible with I and M_1 (K00785); 15 isolated M_1 (K00786–00800); 20 isolated M_2 (K00801–00820); 14 isolated M_3 (K00821–00834).

Horizon O (upper part): 46 isolated M^1 (K00835–00880); 37 isolated M^2 (K00881–00917); 44 isolated M^3 (K00918–00932, 02988–03016); 1 mandible with M_1 (K00933); 2 mandibles without teeth (K00934, 00935); 79 isolated M_1 (K00936–01014); 31 isolated M_2 (K01015–01045); 24 isolated M_3 (K01046–01069).

Horizon N: 49 isolated M^1 (K01070–01118); 49 isolated M^2 (K01119–01167); 33 isolated M^3

Table 50. Holocene fossil localities of *Phaulomys* (restricted to Japan). The numbers on the left side correspond to those in Fig. 120.

LOCALITY	REVISED IDENTIFICATION	REFERENCES	REMARKS
1. Tochibara Rockshelter Site	? <i>Phaulomys</i> cf. <i>smithii</i>	Miyao et al. (1980)	Miyao et al. identified it as <i>Eothenomys kageus</i>
2. Miwa Cave	? <i>Phaulomys</i> cf. <i>smithii</i>	Miyao (1984)	Miyao identified it as <i>Eothenomys kageus</i>
3. Kannondo Cave Site	<i>Phaulomys</i> cf. <i>smithii</i>	Kawamura (1978, 1979a); this paper	In the previous papers, it is identified as <i>Eothenomys smithi</i>
3. Anagami Rockshelter Site	? <i>Phaulomys</i> cf. <i>smithii</i>	This paper	
3. Domen Cave Site	<i>Phaulomys</i> cf. <i>smithii</i>	This paper	
4. Tanuki-ana Cave	<i>Phaulomys</i> cf. <i>smithii</i>	Kawamura & Tamiya (1980); this paper	In the previous paper, it is identified as <i>Eothenomys smithi</i> and / or <i>Aschizomys andersoni</i>
4. Husen-ana Cave	<i>Phaulomys</i> cf. <i>smithii</i>	This paper	
4. Makurazino-ana Cave	<i>Phaulomys</i> cf. <i>smithii</i>	Kowalski & Hasegawa (1976)	Kowalski & Hasegawa identified it as <i>Eothenomys smithi</i>
5. Ninjinkubo First Cave	<i>Phaulomys</i> cf. <i>smithii</i>	Kawamura & Sotsuka (1984); this paper	In the previous paper, it is identified as <i>Eothenomys</i> sp.
5. Yakubono-ana Cave	? <i>Phaulomys</i> cf. <i>smithii</i>	Ditto	Ditto
5. Ojika-do Cave	? <i>Phaulomys</i> cf. <i>smithii</i>	Ditto	Ditto
5. Yoshigadani Third Cave	? <i>Phaulomys</i> cf. <i>smithii</i>	Ditto	Ditto
5. Oiwa-ana Cave	<i>Phaulomys</i> cf. <i>smithii</i>	Ditto	Ditto

(K01168–01200); 2 mandibles with I (K01201, 01202); 7 mandibles without teeth (K01203–01209); 70 isolated M_1 (K01210–01279); 61 isolated M_2 (K01280–01340); 50 isolated M_3 (K01341–01390).

Horizon M (lower part): 33 isolated M^1 (K01391–01423); 21 isolated M^2 (K01424–01444); 15 isolated M^3 (K01445–01459); 1 mandible with M_3 (K01460); 1 mandible with I (K01461); 5 mandibles without teeth (K01462–01466); 51 isolated M_1 (K01467–01517); 29 isolated M_2 (K01518–01546); 24 isolated M_3 (K01547–01570).

Horizon M (upper part): 234 isolated M^1 (K01571–01804); 234 isolated M^2 (K01805–02038); 184 isolated M^3 (K02039–02222); 1 mandible with I, M_1 and M_2 (K02223); 1 mandible with M_1 and M_2 (K02224); 1 mandible with I and M_2 (K02225); 3 mandibles with I (K02226–02228); 13 mandibles without teeth (K02229–02241); 249 isolated M_1 (K02242–02490); 256 isolated M_2 (K02491–02746); 192 isolated M_3 (K02747–02938).

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

2 mandibles with I, M_1 , M_2 and M_3 ; 1 mandible with I.

Mejiro-do Cave (unnumbered specimens of the SOTSUKA Collection)

2 mandibles with I, M_1 , M_2 and M_3 ; 1 mandible with I and M_3 ; 1 mandible with M_1 ; 1 mandible without teeth; 1 isolated M_3 .

HOLOCENE LOCALITIES

Kannondo Cave Site (specimen numbers are prefixed by HUA)

Horizon L: 1 mandible with I, M_1 , M_2 and M_3 (K02939); 1 mandible with I, M_1 and M_2 (K02940); 1 mandible with I (K02941).

Horizon K: 1 skull fragment with left M^1 and M^2 , and with right M^1 and M^2 (K02942); 2 mandibles

with I, M₁ and M₂ (K02943, 02944); 1 mandible without teeth (K02945); 1 isolated M₁ (K02946); 1 isolated M₂ (K02947).

Horizon J: 1 mandible with M₁ and M₂ (K02948); 2 mandibles with I (K02949, 02950); 1 mandible without teeth (K02951); 2 isolated M₃ (K02952, 02953).

Horizon I: 1 skull fragment with M¹ (K02954); 1 maxilla with M¹ and M² (K02955); 1 mandible with I and M₂ (K02956); 1 mandible with M₁ (K02957); 2 mandibles with I (K02958, 02959); 2 mandibles without teeth (K02960, 02961); 3 isolated M₁ (K02962, 02963, 03017); 3 isolated M₂ (K02964–02966) 1 isolated M₃ (K02967).

Horizon H: 1 mandible with M₁ (K02968); 2 mandibles with I (K02969, 02970); 1 isolated M₁ (K02971).

Horizon unknown: 1 skull fragment with left M¹ and right M² (K02972); 1 isolated M¹ (K02973); 1 isolated M² (K02974); 1 mandible with I, M₁ and M₂ (K02975); 1 mandible with I and M₁ (K02976); 1 mandible with M₂ (K02977); 3 mandibles with I (K02978–2980); 1 mandible without teeth (K02981); 1 isolated M₁ (K02982); 1 isolated M₂ (K02983); 4 isolated M₃ (K02984–02987).

Domen Cave Site (specimen numbers are prefixed by HUA)

Horizon V: 10 isolated M¹ (D00002–00011); 14 isolated M² (D00012–00025); 10 isolated M³ (D00026–00035); 13 isolated M₁ (D00036–00048); 11 isolated M₂ (D00049–00059); 8 isolated M₃ (D00060–00067).

Horizon unknown: 1 isolated M¹ (D00068); 1 isolated M³ (D00069).

Tanuki-ana Cave

Layer 4: 1 maxilla with M¹ and M² (ASM 700110); 75 isolated M¹ (ASM 700111–700185); 68 isolated M² (ASM 700186–700253); 47 isolated M³ (ASM 700254–700300); 1 mandible with M₁ (ASM 700301); 3 mandibles without teeth (ASM 700302–700304); 60 isolated M₁ (ASM 700305–700364); 66 isolated M₂ (ASM 700365–700430); 41 isolated M₃ (ASM 700431–700471).

Layer 3: 14 isolated M¹ (ASM 700472–700485); 9 isolated M² (ASM 700486–700494); 9 isolated M³ (ASM 700495–700503); 1 mandible with I, M₁ and M₂ (ASM 700504); 4 mandibles without teeth (ASM 700505–700508); 19 isolated M₁ (ASM 700509–700527); 17 isolated M₂ (ASM 700528–700544); 15 isolated M₃ (ASM 700545–700559).

Layers 3 to 2: 9 isolated M¹ (ASM 700560–700568); 10 isolated M² (ASM 700569–700578); 4 isolated M³ (ASM 700579–700582); 9 isolated M₁ (ASM 700583–700591); 10 isolated M₂ (ASM 700592–700601); 4 isolated M₃ (ASM 700602–700605).

Layer 2: 80 isolated M¹ (ASM 700606–700685); 70 isolated M² (ASM 700686–700755); 78 isolated M³ (ASM 700756–700833); 2 mandibles with I, M₁ and M₂ (ASM 700834, 700835); 2 mandibles with M₁ and M₂ (ASM 700836, 700837); 1 mandible with I and M₁ (ASM 700838); 1 mandible with M₁ (ASM 700839); 3 mandibles without teeth (ASM 700840–700842); 67 isolated M₁ (ASM 700843–700909); 75 isolated M₂ (ASM 700910–700984); 53 isolated M₃ (ASM 700985–701037).

Layer 1: 9 isolated M¹ (ASM 701038–701046); 8 isolated M² (ASM 701047–701054); 11 isolated M³ (ASM 701055–701065); 1 mandible with M₁ (ASM 701066); 7 isolated M₁ (ASM 701067–701073); 5 isolated M₂ (ASM 701074–701078); 11 isolated M₃ (ASM 701079–701089).

Anagami Rockshelter Site

1 isolated M¹ from Layer 3 of Grid B-2 (HUA-A00008).

Husen-ana Cave

1 maxillary fragment (ASM 701090); 42 isolated M¹ (ASM 701091–701132); 37 isolated M² (ASM 701133–701169); 26 isolated M³ (ASM 701170–701195); 1 mandible with I, M₁, M₂ and M₃ (ASM 701196); 1 mandible with I, M₁ and M₂ (ASM 701197); 1 mandible with I, M₂ and M₃ (ASM 701198); 1 mandible with M₁ and M₂ (ASM 701199); 2 mandibles with I and M₁ (ASM 701200, 701201); 1 mandible with I and M₂ (ASM 701202); 1 mandible with I and M₃ (ASM 701203); 2 mandibles with I (ASM 701204, 701205); 6 mandibles without teeth (ASM 701206–701211); 35 isolated M₁ (ASM 701212–701246); 34 isolated M₂ (ASM 701247–701280); 22 isolated M₃ (ASM 701281–701302).

Yoshigatani Third Cave (unnumbered specimens of the Sotsuka Collection)

1 mandible with M₂; 1 isolated M₃.

Ninjinkubo First Cave (unnumbered specimens of the SOTSUKA Collection)

1 skull with left I and M¹, and right M¹ to M³; 1 skull with left I and M², and right M¹ to M³; 2 skulls with I; 3 isolated M¹; 1 isolated M²; 1 isolated M³; 2 mandibles with I, M₁, M₂ and M₃; 1 mandible with I, M₁ and M₂; 1 mandible with I and M₁; 2 mandibles with I; 1 mandible without teeth; 5 isolated M₁; 7 isolated M₂.

Ojika-do Cave (unnumbered specimens of the SOTSUKA Collection)

Chamber 1: 1 mandible with I and M₃.

Chamber 2: 1 mandible with I, M₂ and M₃.

Branch 1: 1 isolated M¹; 2 mandibles with M₁, M₂ and M₃; 1 mandible with I and M₂.

Oiwa-ana Cave (unnumbered specimens of the SOTSUKA Collection)

1 skull with left M¹ to M³ and right M¹; 1 skull with left I and right I; 1 isolated M¹; 1 isolated M²; 5 mandibles with I, M₁, M₂ and M₃; 4 mandibles with I, M₁ and M₂; 1 mandible with I, M₂ and M₃; 1 mandible with I and M₁; 1 mandible with M₂; 2 mandibles with I; 1 isolated M₂.

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

1 skull with left I, M¹ and M², and right I and M¹ to M³.

Description

The morphology of the maxilla and mandible is identical with that of the living *P. smithii* and *P. andersoni* (Fig. 121). The salient angles of the molars are generally rounded. The frequency of closing of the isthmuses is somewhat lower than in *C. japonicus*, but generally as high as, or slightly higher than in the living *P. smithii* and *P. andersoni*. Among the above-listed assemblages of the present form, this frequency is generally higher in the Late Pleistocene assemblages than in the Holocene ones (Tables 51, 52).

In the following description of each molar, several characters are numerically analysed on the Late Pleistocene assemblage of Kannondo Cave Site and the Holocene assemblage of Tanuki-ana Cave, where adequate number of specimen is obtained. The results of the analysis are given in parenthesis. The abbreviations in the parenthesis mean these localities (K=total of Horizons M to P of Kannondo Cave Site; T=total of all the layers of Tanuki-ana Cave).

M¹ —

The anterior loop is followed by four triangles. Three salient angles and two re-entrant angles are observed on each side. LSA4 is always absent. The anterior wall of the anterior loop is usually single-lobed (92.0% of 88 specimens in K; 94.4% of 142 specimens in T), but rarely bilobed. The anterolingual conule is as large as or larger than the anterolabial conule in most specimens (85.2% of 88 specimens in K; 96.5% of 145 specimens in T). The triangles are alternating. T1 and T3 are not so elongated obliquely as in *Microtus*. The isthmuses are usually or often closed (Table 51). However, even if they are open, their widths are not broad. The second minor fold is more or less developed in most specimens (93.4% of 106 specimens in K; 97.3% of 146 specimens in T), while it is not recognized in the remaining specimens. The second secondary fold is unrecognized in more specimens (61.0% of 105 specimens in K; 42.2% of 147 specimens in T). When it is recognized, the degree of the development is generally poor.

M² —

The anterior loop is followed by three triangles. Two and three salient angles are observed on the lingual and buccal sides respectively. LSA4 is always absent as in M¹. The

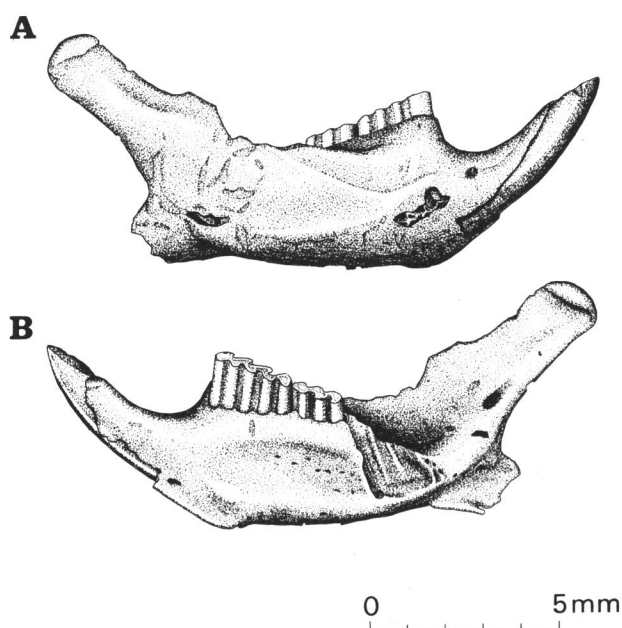


Fig. 121. *Phaulomys* cf. *smithii*. Right mandible with I, M₁, and M₂ from Horizon L of Kannondo Cave Site (HUA-K02940). A, buccal view; B, lingual view.

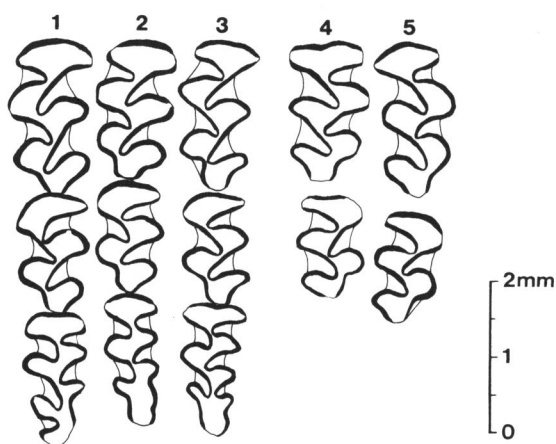


Fig. 122. Upper molar rows of *Phaulomys* cf. *smithii* and the recent *P. smithii*.

1–3, left M¹ to M³ of the recent *P. smithii* (1–2, from Myogata; 3, from Gujohachiman); 4–5, right M¹ and M² of *P. cf. smithii* from Kannondo Cave Site (4, HUA-K02942 from Horizon K; 5, HUA-K02955 from Horizon I).

anterior wall of the anterior loop is almost always single-lobed (95.7% of 93 specimens in K; 98.6% of 146 specimens in T), but it is very rarely bilobed (4.3% in K; 1.4% in T). The triangles are alternating as in M^1 . T3 is hemi-circular or hemi-oval, and not elongated obliquely. Is 2 is usually closed, while Is 3 and Is 4 are often closed (Table 51). The frequencies of closing of the last two isthmuses vary in each fossil assemblage. Namely they are higher in the assemblages of Kannondo Cave Site than in those of Tanuki-ana Cave. The second minor fold is more or less developed in most specimens, but rarely unrecognized (4.2% of 96 specimens in K; 0.7% of 147 specimens in T). The second secondary fold is generally less developed than the second minor fold. Moreover it is unrecognized in higher rate (77.4% of 93 specimens in K; 45.2% of 146 specimens in T).

M^3 —

M^3 generally comprises an anterior loop, three triangles and a posterior loop. Three or

Table 51. Frequency of closing of each isthmus in the upper molars of *Phaulomys* cf. *smithii*, and the recent *P. smithii* and *P. andersoni*. The data of the recent materials are cited from AIMI (1980). The number in parenthesis indicates the total number of the examined specimens.

		<i>Phaulomys</i> Cf. <i>smithii</i>					Recent <i>Phaulomys smithii</i> by Aimi (1980)			Recent <i>Phaulomys andersoni</i> by Aimi (1980)	
		Tanuki-ana Cave		Kannondo Cave Site							
		Layers 1 and 2	Layers 3 and 4	Horizon M	Horizon N	Horizon O	Shikoku	Gozai- sho	Yatsuga- dake	Yatsuga- dake	Chokai
M^1	Is 1	49.2% (65)	54.3% (42)	73.5% (34)	90.0% (10)	80.6% (36)	39.7% (63)	22.2% (27)	8.0% (25)	14.2% (436)	21.7% (23)
	Is 2	44.8 (67)	55.6 (45)	75.7 (37)	100.0 (16)	77.8 (36)	44.4 (63)	44.4 (27)	12.0 (25)	49.5 (436)	65.2 (23)
	Is 3	63.6 (66)	88.9 (46)	91.7 (36)	87.5 (16)	91.7 (36)	41.3 (63)	7.4 (27)	4.0 (25)	27.3 (436)	39.1 (23)
	Is 4	55.4 (56)	56.4 (39)	94.1 (34)	100.0 (17)	65.6 (32)	38.1 (63)	25.9 (27)	16.0 (25)	39.9 (436)	30.4 (23)
M^2	Is 2	85.5 (69)	85.4 (48)	85.2 (27)	100.0 (17)	91.7 (36)	69.8 (63)	70.4 (27)	44.0 (25)	69.7 (436)	91.3 (23)
	Is 3	45.8 (72)	59.6 (47)	74.1 (27)	100.0 (19)	77.8 (36)	47.6 (63)	11.1 (27)	20.0 (25)	63.3 (436)	65.2 (23)
	Is 4	48.4 (64)	63.0 (46)	81.5 (27)	100.0 (18)	81.8 (33)	33.3 (63)	48.1 (27)	8.0 (25)	56.2 (436)	26.1 (23)
M^3	Is 2	86.1 (72)	92.9 (42)	100.0 (19)	100.0 (9)	96.1 (51)	50.8 (63)	51.9 (27)	32.0 (25)	62.6 (436)	56.5 (23)
	Is 3	31.9 (72)	9.5 (42)	20.0 (20)	55.6 (9)	19.2 (52)	12.7 (63)	0 (27)	0 (25)	52.1 (436)	39.1 (23)
	Is 4	75.7 (74)	65.9 (44)	85.0 (20)	77.8 (9)	85.5 (55)	44.4 (63)	63.0 (27)	20.0 (25)	60.1 (436)	34.8 (23)
	Is 5	14.5 (69)	28.6 (42)	63.2 (19)	77.8 (9)	40.7 (54)	19.0 (63)	3.7 (27)	0 (25)	46.6 (436)	39.1 (23)

four salient angles are observed on each side. The anterior wall of the anterior loop is single-lobed or bilobed. The frequency of the former case (57.1% of 84 specimens in K; 68.1% of 116 specimens in T) is somewhat higher than that of the latter case (42.9% in K; 31.9% in T). BRA1 is deep, and only slightly shallower than BRA2. Is 2 is usually closed, while Is 3 is usually or often open (Table 51). When Is 3 is open, T2 and T3 are usually broadly confluent with each other. Is 4 is usually closed, while the frequency of closing of Is 5 varies in each assemblage. Namely the frequency in the assemblage of Kannondo Cave Site is considerably higher than that in Tanuki-ana Cave. When Is 5 is open, T4 is usually broadly confluent with the posterior loop.

The posterior loop is highly variable in shape (Table 44; Fig. 114; Pl. 18). The morphotypes L₁, L₂ and C₁ appear in 10–30% of the total specimens respectively. The frequency of C₂ is somewhat higher (23.6% of 89 specimens in K; 41.2% of 131 specimens in T; 48.3% of 24 specimens in Husen-ana Cave). On the other hand, that of S is much lower (7.9% in K; 3.1% in T; 4.2% in Husen-ana Cave). Moreover F₁, F₂ and Ab are rare or absent in each assemblage.

Although almost all the examined specimens have the above-mentioned characters in common, only one specimen from Horizon P of Kannondo Cave Site exhibits a considerably different pattern (1 of Fig. 116). In this specimen, the crown is remarkably slender, and each re-entrant angle is very shallow. The anterior loop, triangles and posterior loop are broadly confluent with each other to form a continuous dentine field. Each salient angle is strongly rounded. The enamel is rather thin, and the cementum is very poor in each re-entrant angle. Such a pattern is rather similar to that of very old individuals of *Clethrionomys*. In the case of *Clethrionomys*, roots are clearly observed, but the present specimen never exhibits any sign of root-formation.

M₁ —

M₁ comprises an anterior loop, five triangles and a posterior loop as in *C. japonicus*, but its pattern is more variable than in *C. japonicus*. Five salient angles and four re-entrant angles are usually observed on the lingual side. The number of the salient angles rarely decreases to be four (for example, 8, 9, 15, 36 and 37 of Pl. 19). In this case, LRA4 becomes very weak. Exceptionally a small additional salient angle is observed on the anterior face of T5 only in one specimen from Husen-ana Cave (38 of Pl. 19). In this specimen, LRA4 is indistinct and LSA5 is unrecognized, although the number of the salient angles is five. On the buccal side, four salient angles and three re-entrant angles are generally present. An additional re-entrant angle (BRA4) exceptionally appears in a few specimen (for example, 2 of Fig. 116), but it is always weak.

The anterior loop is generally elliptical or hemi-oval. It is sometimes broadly confluent with T5. The relative size of the anterior loop is variable. Namely in some specimens, it is remarkably large (for example, 1, 23, 54, 58 and 62 of Pl. 19), but in other specimen it is small (for example, 17, 26 and 32 of Pl. 19). As regards the general shape of the anterior loop, the morphotype 2 is most frequently found (Table 46; Fig. 115). The frequency of the morphotype 3 is lower than that of 2 in the Late Pleistocene locality (Kannondo Cave Site), while the former

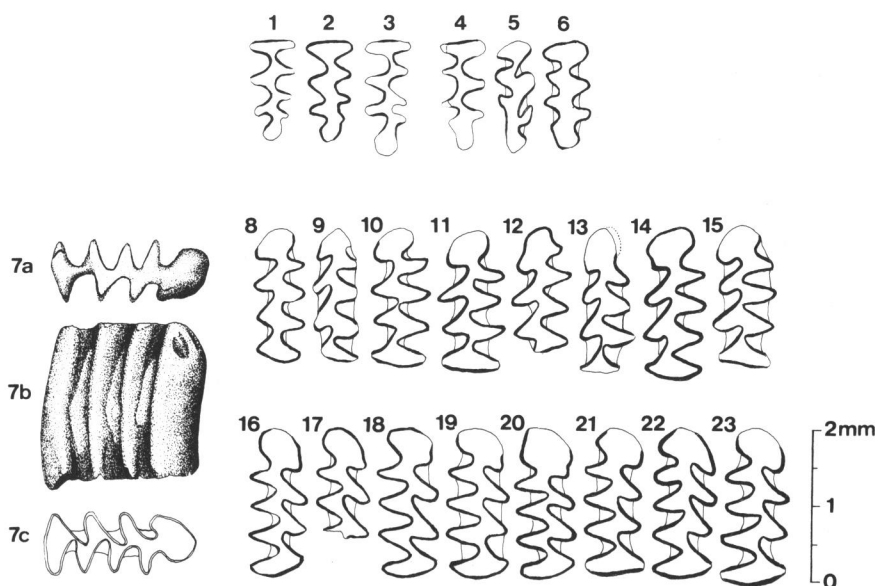


Fig. 123. *Phaulomys* cf. *smithii*. M³ and M₁ of young individuals (1–3, left M³; 4–6, right M³; 7, 16–23, right M₁; 8–15, left M₁).

1, HUA-K03016 from the upper part of Horizon O of Kannondo Cave Site; 2, ASM 700773 from Layer 2 of Tanuki-ana Cave; 3, ASM 701188 from Husen-ana Cave; 4, HUA-K00924 from the upper part of Horizon O of Kannondo Cave Site; 5, 6, ASM 700774, 700775 from Layer 2 of Tanuki-ana Cave; 7, ASM 701241 from Husen-ana Cave (7a, occlusal view; 7b, buccal view; 7c, bottom view); 8, 9, ASM 700854, 700855 from Layer 2 of Tanuki-ana Cave; 10, HUA-K02971 from Horizon H of Kannondo Cave Site; 11, HUA-K02963 from Horizon I of Kannondo Cave Site; 12, 13, ASM 700856, 700857 from Layer 2 of Tanuki-ana Cave; 14, ASM 701242 from Husen-ana Cave; 15, 16, 17, ASM 700858, 700859, 700860 respectively from Layer 2 of Tanuki-ana Cave; 18, ASM 701243 from Husen-ana Cave; 19, HUA-K00800 from the lower part of Horizon O of Kannondo Cave Site; 20, ASM 701244 from Husen-ana Cave; 21, unnumbered specimen from Ninjinkubo First Cave (SOTSUKA Collection); 22, ASM 701245 from Husen-ana Cave; 23, HUA-K02957 from Horizon I of Kannondo Cave Site.

is the same as the latter in the Holocene locality (Husen-ana Cave). On the other hand, the frequency of the morphotype 1 is somewhat higher than that of 3 in Kannondo Cave Site, while the former is much lower than the latter in Husen-ana Cave. The morphotype 4 is found only in low frequency (less than 10%). The anterior wall of the anterior loop is almost always single-lobed, but very rarely bilobed. In young individuals, however, this part is sometimes bilobed or trilobed. The anterolabial conulid is usually as large as or larger than the anterolingual conulid.

The isthmuses other than Is 3 and Is 1 tend to be open (Table 52). The frequency of closing of each isthmus is generally higher in the assemblage of Kannondo Cave Site than in that of Tanuki-ana Cave. Is 6 is almost always or usually open, while Is 5 is usually or often open. When Is 5 is broadly open, T4 and T5 are usually opposed to form a continuous

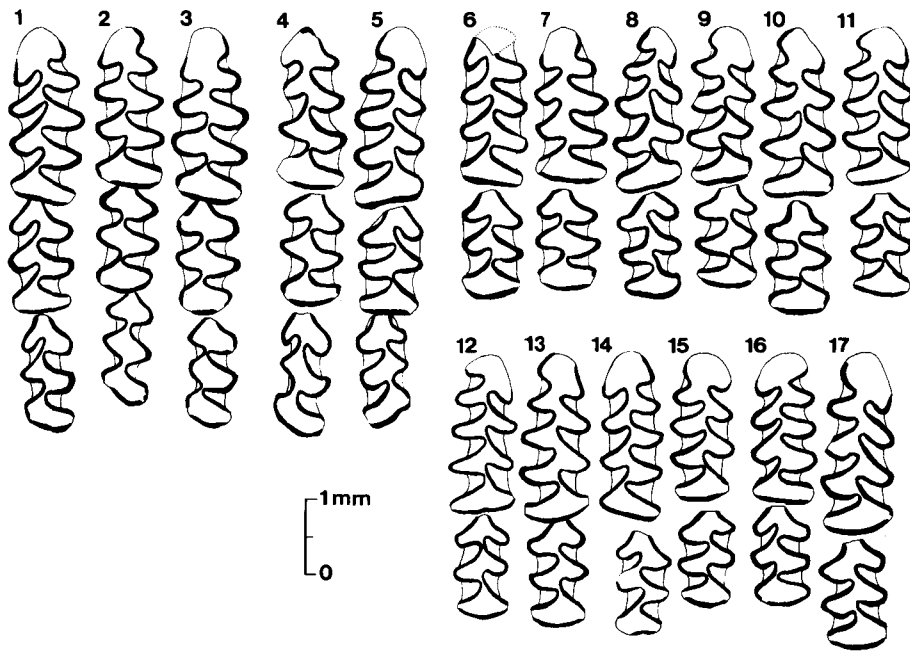


Fig. 124. Lower molar rows of *Phaulomys* cf. *smithii*, *Clethrionomys-Phaulomys* transitional form and the recent *P. smithii*.

1–3, left M_1 to M_3 of the recent *P. smithii* (1, from Gujohachiman; 2–3, from Myogata); 4, left M_1 to M_3 of *P. cf. smithii* from Horizon L of Kannondo Cave Site (HUA-K02939); 5, right M_1 to M_3 of *P. cf. smithii* from Husen-ana Cave (ASM 701196); 6–7, left M_1 and M_2 of *P. cf. smithii* from Kannondo Cave Site (6, HUA-K00784 from the lower part of Horizon O; 7, HUA-K02944 from Horizon K); 8–12, right M_1 and M_2 of *P. cf. smithii* from Kannondo Cave Site (8, HUA-K00783 from the lower part of Horizon O; 9, HUA-K02943 from Horizon K; 10, HUA-K02940 from Horizon L; 11, HUA-K02948 from Horizon J; 12, HUA-K02975=horizon unknown); 13, right M_1 and M_2 of *Clethrionomys-Phaulomys* transitional form from F₂ of Kumaishi-do Cave (YKS 00300); 14–15, left and right M_1 – M_2 of *P. cf. smithii* from Layer 2 of Tanuki-ana Cave (14, ASM 700836; 15, ASM 700837); 16–17, left and right M_1 – M_2 of *P. cf. smithii* from Husen-ana Cave (16, ASM 701197; 17, ASM 701199).

dentine field which extends obliquely (for example, 10, 13, 14, 21, 34, 36, 48 and 59 of Pl. 19). Is 4 is sometimes or often closed. When this isthmus is open, a continuous dentine field is sometimes formed by the confluence of T3 and T4, which extends rather transversely (for example, 30 and 45 of Pl. 19). Is 3 is usually closed, while Is 2 is almost always or usually open. When Is 2 is open, T1 and T2 are usually well confluent with each other to form a wide dentine field as in the case of T3 and T4 (for example 12, 16, 23, 28, 30, 34, 37, 41, 44, 45, 48, 54, 57 and 68 of Pl. 19). Is 1 is almost always closed.

The posterior wall of the posterior loop is single-lobed in most specimens (90.0% of 242 specimens in K; 94.7% of 113 specimens in T), while it is bilobed in the remaining specimens.

Table 52. Frequency of closing of each isthmus in the lower molars of *Phaulomys* cf. *smithii*, and the recent *P. smithii* and *P. andersoni*. The data of the recent materials are cited from AIMI (1980). The number in parenthesis indicates the total number of the examined specimens.

		<i>Phaulomys</i> cf. <i>smithii</i>					Recent <i>Phaulomys smithii</i> by Aimi (1980)			Recent <i>Phaulomys andersoni</i> by Aimi (1980)	
		Tanuki-ana Cave		Kannondo Cave Site			Shikoku	Gozai-sho	Yatsugadake	Yatsugadake	Chokai
		Layers 1 and 2	Layers 3 and 4	Horizon M	Horizon N	Horizon O					
M_1	Is 6	4.0% (50)	1.9% (54)	5.0% (141)	12.0% (50)	13.9% (72)	0% (63)	0% (27)	0% (25)	3.4% (436)	4.3% (23)
	Is 5	17.0 (53)	9.3 (54)	33.6 (143)	50.9 (53)	15.1 (73)	0 (63)	7.4 (27)	4.0 (25)	2.8 (436)	0 (23)
	Is 4	24.5 (53)	20.8 (53)	41.7 (144)	64.2 (53)	74.3 (74)	27.0 (63)	0 (27)	0 (25)	41.5 (436)	34.8 (23)
	Is 3	75.5 (53)	69.8 (53)	90.1 (141)	90.7 (54)	90.8 (86)	34.9 (63)	55.6 (27)	24.0 (25)	54.1 (436)	34.8 (23)
	Is 2	3.9 (51)	0 (51)	12.5 (128)	32.7 (52)	25.3 (75)	6.3 (63)	0 (27)	0 (25)	24.1 (436)	26.1 (23)
	Is 1	97.8 (45)	100.0 (49)	99.2 (125)	100.0 (50)	98.6 (73)	69.8 (63)	88.9 (27)	44.0 (25)	70.4 (436)	56.5 (23)
M_2	Is 4	0 (60)	0 (50)	2.7 (37)	5.3 (19)	0 (29)	0 (63)	0 (27)	0 (25)	0.2 (436)	0 (23)
	Is 3	100.0 (65)	98.1 (53)	100.0 (39)	100.0 (20)	100.0 (33)	76.2 (63)	92.6 (27)	44.0 (25)	81.7 (436)	78.3 (23)
	Is 2	0 (66)	0 (54)	5.1 (39)	15.0 (20)	3.0 (33)	0 (63)	0 (27)	0 (25)	12.2 (436)	4.3 (23)
	Is 1	100.0 (67)	100.0 (52)	100.0 (40)	100.0 (22)	100.0 (33)	88.9 (63)	88.9 (27)	44.0 (25)	82.8 (436)	87.0 (23)
M_3	Is 4	0 (51)	0 (38)	0 (30)	0 (19)	0 (27)	0 (63)	0 (27)	0 (25)	0.2 (436)	0 (23)
	Is 3	96.2 (52)	97.4 (39)	100.0 (30)	100.0 (20)	100.0 (30)	87.3 (63)	92.6 (27)	52.0 (25)	82.6 (436)	82.6 (23)
	Is 2	0 (52)	0 (39)	0 (29)	0 (20)	0 (30)	0 (63)	0 (27)	0 (25)	1.1 (436)	0 (23)
	Is 1	98.1 (52)	100.0 (38)	100.0 (30)	100.0 (19)	100.0 (31)	93.7 (63)	100.0 (27)	48.0 (25)	84.4 (436)	91.3 (23)

Exceptionally, one specimen from the upper part of Horizon O of Kannondo Cave Site shows a very unusual pattern (3 of Fig. 116). In this specimen, the anterior loop is triangular, whose dentine field is confluent with those of T4 and T5. T5 is very small, which is also connected with T3. BRA2 is excessively developed and bifurcated. T3 is well separated from T4 by the anterior branch of BRA2. LRA3 is remarkably weak.

M_2 —

M_2 comprises four triangles and a posterior loop. Three salient angles and two re-entrant angles are observed on each side. The first secondary fold is often or usually recognizable

(69.0% of 100 specimens in K; 78.7% of 150 specimens in T), but its concavity is mostly weak. The anterior labial fold is usually unrecognized (89.7% of 97 specimens in K; 72.3% of 148 specimens in T). Even if this fold is recognized, it is usually weak. The triangles are somewhat less alternating than in *C. japonicus*. Is 4 is almost always open (Table 52), and its width is usually broad. In a few specimens, however, it is narrowed by deep intrusion of BRA2 (for example, 4 of Fig. 116). Is 3 is almost always closed, while Is 2 is almost always open. In most specimens, T1 is opposite to T2, and the dentine fields of these triangles are well confluent with each other. Is 1 is always closed. The posterior wall of the posterior loop is almost always single-lobed (97.2% of 107 specimens in K; 99.3% of 152 specimens in T).

*M*₃—

*M*₃ comprises two dentine fields and a posterior loop which are set obliquely. Three salient angles and two re-entrant angles are observed on each side. The buccal re-entrant angles are shallower than the lingual ones. The first secondary fold is usually or often unrecognized (76.7% of 86 specimens in K; 63.2% of 114 specimens in T). When this fold is recognized, it is usually weak. The anterior labial fold is almost always or usually lacking (97.6% of 85 specimens in K; 89.6% of 115 specimens in T). Even if this fold is recognized, its concavity is always slight. Is 4 and Is 2 are always open, whereas Is 3 and Is 1 are almost always closed (Table 52). The posterior wall of the posterior loop is single-lobed in most specimens (95.4% of 87 specimens in K; 98.2% of 109 specimens in T), but it is bilobed in the remaining specimens.

Measurements

The measurements of the mandibles and molars are given in Tables 53 and 54–59 respectively.

Table 53. Measurements of the mandibles of *Phaulomys* cf. *smithii* from Kannondo Cave Site in mm. The numbers on the left side correspond to those in Fig. 72.

	Horizon unknown		Horizon I		Horizon J		Horizon K				Horizon O (lower part)	
	HUA-K 02976	HUA-K 02977	HUA-K 02956	HUA-K 02948	HUA-K 02943	HUA-K 02944	HUA-K 02940	HUA-K 02939	HUA-K 00783	HUA-K 00785		
2. Total length of the mandible (id to the condyle)	14.51±	14.68	—	—	—	—	—	—	—	—		
3. Length from the tip of the incisor to the condyle	16.38	—	—	—	—	—	—	—	—	—		
4. Length of the horizontal ramus	8.66±	9.34	—	—	—	—	—	—	—	—		
6. Length of the ascending ramus (the posterior border of <i>M</i> ₃ to the condyle)	6.66	6.56	—	5.71±	—	—	—	—	—	—		
8. Height of the ascending ramus (gov to the highest point of the condyle)	—	7.27	—	6.51±	—	—	—	—	—	—		
10. Ditto (gov to the mandibular incision)	—	5.40	—	—	—	—	—	—	—	—		
12. Maximum height of the horizontal ramus	—	—	3.23	—	3.10	—	3.16	3.39	—	3.17		
14. Maximum thickness of the horizontal ramus	2.47	2.38	2.53	—	2.08	—	2.27	2.56	—	2.31		
15. Length of the molar row (<i>M</i> ₁ to <i>M</i> ₃) at the crowns	—	—	—	—	—	—	—	5.60	—	—		
16. Ditto at the alveoli	—	—	—	5.40	—	—	—	5.81±	—	—		
17. Length of the molar row (<i>M</i> ₁ to <i>M</i> ₂) at the crowns	—	—	—	3.62	3.51	3.47	3.88	3.76	3.65	—		
18. Ditto at the alveoli	—	—	4.25±	3.73	3.80	3.65	4.02	3.80±	3.91±	—		

Table 54. Measurements of M^1 of *Phaulomys* cf. *smithii*, and the recent *P. andersoni* and *P. smithii* in mm. * AIMI Collection; ** partly AIMI Collection; ○ SOTSUKA Collection; Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
<i>Phaulomys andersoni</i>										
Mt. Chokai*	5	2.15	2.20	2.29	0.05	5	0.94	1.10	1.19	0.09
Mt. Yatsugadake**	48	1.98	2.24	2.47	0.10	47	1.15	1.28	1.42	0.07
<i>Phaulomys smithii</i>										
Myogata	4	1.75	1.87	2.02	—	4	0.87	1.02	1.09	—
Gujohachiman	3	2.02	2.03	2.03	—	3	1.04	1.08	1.12	—
Mikawa Heights	13	1.79	1.95	2.22	0.11	13	0.95	1.09	1.17	0.05
Sakuma	2	1.86	1.90	1.94	—	2	1.07	1.09	1.12	—
Mt. Tsurugi*	28	1.74	1.95	2.16	0.11	28	0.96	1.09	1.24	0.06
HOLOCENE (<i>P. cf. smithii</i>)										
Yakubono-ana Cave°	2	1.80	1.80	1.80	—	2	0.94	0.94	0.94	—
Oiwa-ana Cave°	3	1.79	1.85	1.88	—	3	0.95	0.98	1.00	—
Ojika-do Cave (Branch 1)°	1	—	1.90	—	—	1	—	1.09	—	—
Ninjinkubo First Cave°	6	1.86	1.95	2.12	0.11	6	0.92	1.02	1.10	0.06
Husen-ana Cave	36	1.70	1.89	2.10	0.10	35	0.93	1.04	1.24	0.06
Tanuki-ana Cave										
Layer 1	9	1.74	1.88	2.07	0.10	9	0.90	1.00	1.17	0.08
Layer 2	48	1.58	1.87	2.19	0.12	56	0.79	0.99	1.14	0.06
Layers 2 to 3	5	1.76	1.93	2.19	0.16	5	0.96	1.05	1.14	0.07
Layer 3	6	1.63	1.85	2.00	0.13	6	0.89	1.02	1.07	0.06
Layer 4	33	1.60	1.88	2.15	0.13	39	0.79	1.00	1.18	0.09
Domen Cave Site										
Horizon unknown	—	—	—	—	—	1	—	1.02	—	—
Horizon V	6	1.60	1.88	2.13	0.17	8	0.93	1.04	1.16	0.09
Kannondo Cave Site										
Horizon unknown	1	—	1.83	—	—	1	—	0.95	—	—
Horizon I	2	1.98	2.02	2.06	—	2	1.05	1.07	1.08	—
Horizon K	2	1.84	1.85	1.86	—	2	1.03	1.06	1.09	—
LATE PLEISTOCENE (<i>P. cf. smithii</i>)										
Kannondo Cave Site										
Horizon M (upper)	15	1.76	1.94	2.19	0.12	17	0.95	1.04	1.12	0.05
Horizon M (lower)	15	1.80	1.96	2.35	0.16	16	0.94	1.09	1.30	0.09
Horizon N	8	1.83	1.97	2.15	0.10	9	0.96	1.08	1.17	0.07
Horizon O (upper)	22	1.65	2.02	2.22	0.15	25	0.93	1.12	1.33	0.08
Horizon O (lower)	7	1.95	2.16	2.46	0.17	8	1.10	1.19	1.30	0.05
Horizon P	1	—	1.88	—	—	2	0.99	1.08	1.17	—
Seiryukutsu Cave	3	1.81	1.93	2.08	—	3	0.97	1.03	1.09	—

Comparison and Discussion

The present fossils are distinguishable from *Clethrionomys* in having unrooted molars, although a member of this group (*C. japonicus*) has similar patterns of molars. The voles with unrooted molars such as *Hyperacrius*, *Alticola*, *Eothenomys* and *Phaulomys* are considered to be closely related to *Clethrionomys*. Of these genera, the present fossils are clearly distinct from *Hyperacrius* and *Alticola* in the following characters:

1. The cementum in each re-entrant angle is better developed than in both of these genera.
2. The re-entrant folds of M^3 and M_3 are somewhat narrower than in *Alticola*.
3. M^3 shows a more complicate pattern than in *Hyperacrius* where T4 is unrecognized.
4. BRA 1 of M^3 is much deeper than in both genera.
5. In M_1 , the number of closed triangles is more than that of *Hyperacrius* (only one in this genus).

The genus *Eothenomys* includes several species with various types of molars. Although the

Table 55. Measurements of M^2 of *Phaulomys* cf. *smithii*, and the recent *P. andersoni* and *P. smithii* in mm. Symbols and abbreviations as in Tables 54 and 38 respectively.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
<i>Phaulomys andersoni</i>										
Mt. Chokai*	5	1.55	1.62	1.71	0.06	5	0.94	0.99	1.10	0.06
Mt. Yatsugadake**	48	1.45	1.66	1.78	0.07	48	0.90	1.07	1.21	0.06
<i>Phaulomys smithii</i>										
Myogata	4	1.35	1.47	1.57	—	4	0.82	0.89	0.97	—
Gujohachiman	3	1.49	1.54	1.61	—	3	0.90	0.90	0.91	—
Mikawa Heights	13	1.34	1.46	1.60	0.06	13	0.86	0.95	1.01	0.04
Sakuma	2	1.46	1.48	1.50	—	2	0.91	0.92	0.94	—
Mt. Tsurugi	29	1.32	1.46	1.59	0.07	29	0.85	0.97	1.06	0.05
HOLOCENE (<i>P. cf. smithii</i>)										
Yakubono-ana Cave°	2	1.36	1.37	1.38	—	2	0.80	0.82	0.85	—
Oiwa-ana Cave°	2	1.41	1.42	1.43	—	2	0.84	0.84	0.85	—
Ninjinkubo First Cave°	4	1.45	1.52	1.62	—	4	0.88	0.90	0.97	—
Husen-ana Cave	36	1.31	1.47	1.57	0.06	36	0.83	0.92	1.05	0.06
Tanuki-ana Cave										
Layer 1	5	1.39	1.48	1.59	0.07	6	0.83	0.91	1.02	0.06
Layer 2	50	1.24	1.43	1.60	0.08	59	0.66	0.87	1.01	0.07
Layers 2 to 3	7	1.36	1.43	1.58	0.07	9	0.84	0.87	0.92	0.03
Layer 3	8	1.24	1.46	1.66	0.13	7	0.79	0.90	0.95	0.05
Layer 4	36	1.28	1.45	1.66	0.09	40	0.73	0.88	1.09	0.08
Domen Cave Site										
Horizon V	7	1.42	1.49	1.58	0.05	12	0.83	0.90	0.97	0.04
Kannondo Cave Site										
Horizon unknown	—	—	—	—	—	1	—	0.86	—	—
Horizon I	1	—	1.50	—	—	1	—	0.91	—	—
Horizon K	2	1.36	1.37	1.37	—	2	0.89	0.91	0.93	—
LATE PLEISTOCENE (<i>P. cf. smithii</i>)										
Kannondo Cave Site										
Horizon M (upper)	17	1.33	1.46	1.56	0.06	21	0.80	0.89	1.03	0.05
Horizon M (lower)	3	1.43	1.48	1.50	—	3	0.86	0.88	0.91	—
Horizon N	10	1.38	1.50	1.66	0.09	15	0.81	0.91	1.07	0.07
Horizon O (upper)	20	1.39	1.52	1.64	0.07	23	0.73	0.91	1.02	0.07
Horizon O (lower)	12	1.40	1.60	1.74	0.08	12	0.82	0.95	1.05	0.06
Horizon P	6	1.44	1.52	1.64	0.08	10	0.73	0.91	1.02	0.08
Seiryukutsu Cave	2	1.37	1.49	1.60	—	2	0.90	0.94	0.99	—

limits of the genus are still controversial, at least seven species can be allocated to this genus. They are *Eothenomys melanogaster* (MILNE-EDWARDS, 1872), *E. olitor* (THOMAS, 1911), *E. proditor* HINTON, 1923, *E. chinensis* (THOMAS, 1891), *E. custos* (THOMAS, 1912), *E. inez* (THOMAS, 1908), *E. eva* (THOMAS, 1911).

Of these species, *E. melanogaster* differs from the present fossils in having LSA4 in M^1 and M^2 , and more complicate anterior loop in M_1 . *E. olitor* and *E. proditor* also differ in having LSA4 in M^2 , shallower BRA1 in M^3 , and more complicate and larger anterior loop in M_1 . *E. chinensis* and *E. custos* are distinguishable from the present fossils by usual development of LSA4 in M^2 , more complicate pattern of M^3 , and shallower BRA1 of the same molar. *E. inez* and *E. eva* are also distinguishable by the presence of weak LSA4 in M^2 , different shapes of the anterior loop in M_1 and closed Is 2 of M_2 . Therefore the present fossils are distinct from *Eothenomys*, as far as these species are concerned.

The species of the genus *Phaulomys*, *P. smithii* and *P. andersoni*, have great resemblance to the present fossils in osteological and dental characters, and no significant differences can be found

Table 56. Measurements of M^3 of *Phaulomys* cf. *smithii*, and the recent *P. andersoni* and *P. smithii* in mm. Symbols and abbreviations as in Tables 54 and 38 respectively.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
<i>Phaulomys andersoni</i>										
Mt. Chokai*	5	1.81	1.94	2.04	0.08	5	0.88	0.90	0.92	0.02
Mt. Yatsugadake**	48	1.75	2.06	2.41	0.14	48	0.85	0.99	1.09	0.06
<i>Phaulomys smithii</i>										
Myogata	4	1.64	1.73	1.77	—	4	0.72	0.77	0.85	—
Gujohachiman	3	1.62	1.79	1.96	—	3	0.79	0.84	0.88	—
Mikawa Heights	12	1.62	1.78	1.88	0.09	12	0.79	0.84	0.95	0.05
Sakuma	2	1.81	1.81	1.82	—	2	0.78	0.79	0.80	—
Mt. Tsurugi*	29	1.61	1.75	1.90	0.08	29	0.76	0.86	0.96	0.05
HOLOCENE (<i>P. cf. smithii</i>)										
Yakubono-ana Cave°	1	—	1.79	—	—	1	—	0.70	—	—
Oiwa-ana Cave°	1	—	1.75	—	—	1	—	0.73	—	—
Ninjinkubo First Cave°	3	1.68	1.83	2.06	—	3	0.80	0.84	0.89	—
Husen-ana Cave	26	1.44	1.67	1.85	0.09	26	0.70	0.81	0.90	0.04
Tanuki-ana Cave										
Layer 1	9	1.57	1.72	1.87	0.09	9	0.71	0.77	0.82	0.04
Layer 2	53	1.46	1.67	1.98	0.12	61	0.63	0.77	0.98	0.06
Layers 2 to 3	2	1.51	1.71	1.92	—	2	0.64	0.73	0.81	—
Layer 3	7	1.61	1.70	1.86	0.08	7	0.74	0.77	0.87	0.04
Layer 4	31	1.37	1.70	1.95	0.15	34	0.60	0.77	0.87	0.07
Domen Cave Site										
Horizon unknown	1	—	1.75	—	—	1	—	0.87	—	—
Horizon V	6	1.61	1.74	1.83	0.07	7	0.71	0.80	0.86	0.05
LATE PLEISTOCENE (<i>P. cf. smithii</i>)										
Kannondo Cave Site										
Horizon M (upper)	12	1.46	1.73	2.00	0.14	12	0.70	0.80	0.86	0.05
Horizon M (lower)	5	1.49	1.76	1.92	0.16	6	0.78	0.81	0.87	0.03
Horizon N	7	1.68	1.78	2.01	0.11	8	0.75	0.81	0.92	0.06
Horizon O (upper)	32	1.43	1.75	2.01	0.11	40	0.67	0.81	0.96	0.06
Horizon O (lower)	8	1.62	1.80	1.99	0.11	9	0.78	0.85	0.93	0.04
Horizon P	2	1.89	1.90	1.91	—	3	0.82	0.86	0.95	—
Yage Quarry										
Site 4	1	—	1.85	—	—	1	—	0.86	—	—

between them. This fact indicates that the present fossils can be allocated to *Phaulomys* instead of the above-mentioned genera.

The two living species of *Phaulomys* are very similar to each other in osteological and dental characters. As regards the differences between them in these characters, TOKUDA (1968) paid attention to the relative size of the anterior loop of M_1 . He stated that the anterior loop was smaller in *P. andersoni* than in *P. smithii*. On the other hand, AIMI (1980) provided useful data on other morphological differences between the molars of these species. His data show that Is 3 and Is 5 of M^3 , and Is 2 and Is 4 of M_1 are more frequently closed in *P. andersoni* than in *P. smithii* (see Tables 51, 52). In addition to these, the measurements of the recent specimens by the present author and by HANAMURA *et al.* (1975) indicate that the molars of *P. andersoni* are generally larger than those of *P. smithii* (Tables 54–59). However all of these differences are useless for the specific distinction of each individual, because there are considerable overlaps in appearance of each character between these two species. Therefore the allocation of each fossil specimen to one of these species is logically impossible. Although KOWALSKI and HASEGAWA (1976) distinguished *smithii* from *andersoni* in the description of the Japanese fossil rodents, their distinction has no grounds from the viewpoints of the present paper. The author believes it

Table 57. Measurements of M_1 of *Phaulomys* cf. *smithii*, and the recent *P. andersoni* and *P. smithii* in mm. ○○ MATSUHASHI Collection; other symbols and abbreviations as in Tables 54 and 38 respectively.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
<i>Phaulomys andersoni</i>										
Mt. Chokai*	5	2.35	2.49	2.59	0.08	5	1.02	1.08	1.14	0.05
Mt. Yatsugadake**	46	2.33	2.55	2.97	0.11	48	1.01	1.15	1.31	0.06
<i>Phaulomys smithii</i>										
Myogata	4	2.08	2.22	2.33	—	4	0.87	0.98	1.10	—
Gujohachiman	3	2.31	2.36	2.40	—	3	0.90	0.97	1.01	—
Mikawa Heights	13	2.15	2.32	2.69	0.14	13	0.88	1.02	1.14	0.07
Sakuma	2	2.23	2.24	2.25	—	2	0.97	1.01	1.06	—
Mt. Tsurugi*	25	2.09	2.28	2.42	0.09	29	0.92	1.02	1.14	0.06
HOLOCENE (<i>P. cf. smithii</i>)										
Oiwa-ana Cave°	10	2.04	2.16	2.28	0.08	10	0.82	0.90	0.97	0.05
Ojika-do Cave (Branch 1)°	2	2.15	2.21	2.28	—	2	0.94	0.96	0.98	—
Ninjinkubo First Cave°	8	1.96	2.12	2.31	0.11	9	0.81	0.95	1.12	0.08
Husen-ana Cave	30	1.96	2.19	2.50	0.14	31	0.78	0.95	1.11	0.08
Tanuki-ana Cave										
Layer 1	3	1.99	2.14	2.24	—	4	0.85	0.88	0.95	—
Layer 2	38	1.79	2.15	2.44	0.15	55	0.67	0.90	1.02	0.08
Layers 2 to 3	3	2.09	2.19	2.30	—	4	0.88	0.93	1.00	—
Layer 3	16	1.87	2.21	2.39	0.12	18	0.83	0.92	0.99	0.05
Layer 4	34	1.86	2.19	2.44	0.16	37	0.79	0.93	1.08	0.07
Domen Cave Site										
Horizon V	5	2.16	2.25	2.32	0.06	8	0.88	0.97	1.05	0.06
Kannondo Cave Site										
Horizon unknown	2	2.09	2.23	2.36	—	2	0.88	0.89	0.90	—
Horizon H	1	—	2.30	—	—	1	—	0.98	—	—
Horizon I	4	1.87	2.17	2.43	—	4	0.93	0.98	1.04	—
Horizon J	1	—	2.16	—	—	1	—	0.94	—	—
Horizon K	3	2.09	2.16	2.29	—	3	0.89	0.99	1.08	—
Horizon L	2	2.17	2.22	2.26	—	2	0.97	0.99	1.01	—
LATE PLEISTOCENE (<i>P. cf. smithii</i>)										
Mejiro-do Cave°	4	2.02	2.16	2.25	—	4	0.85	0.89	0.94	—
Suse Quarry (East Fissure)°°	2	2.00	2.03	2.07	—	2	0.93	0.94	0.95	—
Kannondo Cave Site										
Horizon M (upper)	86	1.93	2.16	2.44	0.13	104	0.79	0.94	1.11	0.07
Horizon M (lower)	24	1.88	2.19	2.58	0.17	27	0.79	0.96	1.05	0.07
Horizon N	37	2.00	2.30	2.58	0.12	48	0.88	0.98	1.16	0.05
Horizon O (upper)	45	2.05	2.35	2.62	0.14	52	0.88	1.00	1.15	0.06
Horizon O (lower)	12	2.02	2.32	2.72	0.18	14	0.86	0.98	1.11	0.06
Horizon P	3	2.27	2.39	2.54	—	7	0.91	0.99	1.10	0.06
Seiryukutsu Cave	4	2.12	2.15	2.19	—	4	0.90	0.92	0.94	—

most desirable that the definite specific determination is reserved or only "confer" determination is given to the fossil specimens referable to *Phaulomys* (see Tables 49, 50).

The detailed analysis of the variation in size and molar pattern of the present fossils shows that the assemblages from the Holocene localities rather resemble *P. smithii* both in size and pattern, while those from the Late Pleistocene localities are rather similar to *P. smithii* in size, and to *P. andersoni* in pattern. Because the differences between both assemblages are however slight, the present fossils are assigned to *P. cf. smithii* altogether.

As already pointed out, the two living species of *Phaulomys* are derived in common from *Clethrionomys japonicus* through *Clethrionomys-Phaulomys* transitional form (Fig. 118). The oldest record of *Phaulomys* cf. *smithii* is obtained from the lowest layer of Kannondo Cave Site (Horizon P). On the other hand, the youngest record of *Clethrionomys-Phaulomys* transitional form is from

Table 58. Measurements of M_2 of *Phaulomys* cf. *smithii*, and the recent *P. andersoni* and *P. smithii* in mm. ○○ MATSUHASHI Collection; other symbols and abbreviations as in Tables 54 and 38 respectively.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
<i>Phaulomys andersoni</i>										
Mt. Chokai*	5	1.54	1.58	1.64	0.04	5	0.94	0.97	1.04	0.04
Mt. Yatsugadake**	48	1.48	1.66	1.79	0.07	48	0.92	1.03	1.30	0.06
<i>Phaulomys smithii</i>										
Myogata	4	1.32	1.46	1.58	—	4	0.80	0.86	0.98	—
Gujohachiman	3	1.52	1.55	1.59	—	3	0.83	0.87	0.90	—
Mikawa Heights	13	1.38	1.49	1.67	0.08	13	0.77	0.90	0.95	0.05
Sakuma	2	1.49	1.49	1.50	—	2	0.86	0.89	0.91	—
Mt. Tsurugi*	29	1.32	1.43	1.54	0.06	29	0.81	0.90	1.02	0.05
HOLOCENE (<i>P. cf. smithii</i>)										
Oiwa-ana Cave°	12	1.28	1.36	1.47	0.06	12	0.74	0.79	0.89	0.05
Ojika-do Cave°										
Chamber 2	1	—	1.45	—	—	1	—	0.89	—	—
Branch 1	3	1.31	1.36	1.41	—	3	0.77	0.80	0.82	—
Ninjinkubo First Cave°	10	1.24	1.35	1.52	0.08	10	0.69	0.80	0.88	0.06
Yoshigadani Third Cave°	1	—	1.30	—	—	1	—	0.75	—	—
Husen-ana Cave	35	1.27	1.41	1.58	0.08	35	0.70	0.83	0.95	0.06
Tanuki-ana Cave										
Layer 1	4	1.26	1.32	1.38	—	5	0.66	0.77	0.88	0.08
Layer 2	52	1.24	1.38	1.51	0.08	65	0.63	0.80	0.91	0.06
Layers 2 to 3	5	1.20	1.40	1.54	0.12	9	0.71	0.80	0.94	0.08
Layer 3	13	1.19	1.37	1.63	0.12	16	0.70	0.81	1.00	0.08
Layer 4	34	1.18	1.38	1.64	0.11	43	0.63	0.80	0.92	0.07
Domen Cave Site										
Horizon V	9	1.30	1.40	1.50	0.07	11	0.76	0.85	0.91	0.05
Kannondo Cave Site										
Horizon unknown	2	1.38	1.47	1.56	—	3	0.75	0.82	0.90	—
Horizon I	4	1.31	1.40	1.64	—	4	0.73	0.88	0.98	—
Horizon J	1	—	1.41	—	—	1	—	0.85	—	—
Horizon K	3	1.35	1.36	1.38	—	3	0.82	0.87	0.90	—
Horizon L	2	1.50	1.51	1.52	—	2	0.86	0.88	0.90	—
LATE PLEISTOCENE (<i>P. cf. smithii</i>)										
Mejiro-do Cave°	1	—	1.36	—	—	1	—	0.76	—	—
Suse Quarry (East Fissure)°°	2	1.34	1.38	1.42	—	2	0.77	0.80	0.83	—
Kannondo Cave Site										
Horizon M (upper)	26	1.30	1.41	1.57	0.07	26	0.74	0.86	0.94	0.05
Horizon M (lower)	6	1.34	1.43	1.54	0.07	12	0.65	0.86	0.96	0.08
Horizon N	14	1.28	1.46	1.70	0.13	19	0.70	0.85	1.00	0.07
Horizon O (upper)	13	1.42	1.55	1.67	0.07	15	0.82	0.91	0.96	0.04
Horizon O (lower)	10	1.33	1.49	1.65	0.11	13	0.75	0.88	1.07	0.08
Horizon P	5	1.39	1.57	1.78	0.15	5	0.85	0.93	1.00	0.06
Seiryukutsu Cave	1	—	1.39	—	—		—	0.81	—	—

F₄ of Kumaishi-do Cave. From the radiometric dates and other evidences, the former record is considered to be older than the latter. The temporal relationship between these records is seemingly inconsistent with the evolutionary trend of this group. However it can be interpreted as a time lag of the transition from *Clethrionomys-Phaulomys* transitional form to *Phaulomys* in each area. Namely, the transition did not take place concurrently in each area. Such a phenomenon seems to be rather natural, when animals undergo gradual evolution.

Until the beginning of Holocene, this transition was completed. It can be demonstrated by the fact that rooted molars of this group are never found in the Holocene sediments in Honshu, Shikoku and Kyushu, and all the fossils from these sediments are therefore identified as *Phaulomys* (mostly as *P. cf. smithii*).

Table 59. Measurements of M_3 of *Phaulomys* cf. *smithii*, and the recent *P. andersoni* and *P. smithii* in mm. ○○ MATSUHASHI Collection; other symbols and abbreviations as in Tables 54 and 38 respectively.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
<i>Phaulomys andersoni</i>										
Mt. Chokai*	5	1.60	1.69	1.77	0.06	5	0.76	0.83	0.89	0.05
Mt. Yatsugadake**	48	1.40	1.73	1.89	0.11	48	0.73	0.86	1.01	0.06
<i>Phaulomys smithii</i>										
Myogata	4	1.41	1.53	1.72	—	4	0.67	0.71	0.74	—
Gujohachiman	3	1.52	1.57	1.60	—	3	0.69	0.73	0.77	—
Mikawa Heights	12	1.42	1.52	1.73	0.09	12	0.67	0.73	0.81	0.04
Sakuma	2	1.43	1.48	1.53	—	2	0.72	0.74	0.75	—
Mt. Tsurugi*	29	1.31	1.51	1.71	0.09	29	0.66	0.75	0.82	0.04
HOLOCENE (<i>P. cf. smithii</i>)										
Oiwa-ana Cave°	6	1.29	1.40	1.53	0.09	6	0.62	0.67	0.70	0.03
Ojika-do Cave°										
Chamber 1	1	—	1.52	—	—	1	—	0.70	—	—
Chamber 2	1	—	1.53	—	—	1	—	0.68	—	—
Branch 1	2	1.36	1.39	1.43	—	2	0.68	0.69	0.70	—
Ninjinkubo First Cave°	2	1.27	1.30	1.34	—	2	0.65	0.67	0.70	—
Yoshigadani Third Cave°	1	—	1.29	—	—	1	—	0.63	—	—
Husen-ana Cave	20	1.29	1.43	1.60	0.09	21	0.58	0.70	0.76	0.04
Tanuki-ana Cave										
Layer 1	8	1.12	1.38	1.60	0.14	8	0.56	0.66	0.73	0.06
Layer 2	43	1.20	1.40	1.65	0.12	44	0.48	0.66	0.78	0.05
Layers 2 to 3	2	1.44	1.47	1.50	—	3	0.63	0.67	0.70	—
Layer 3	9	1.26	1.40	1.56	0.10	13	0.59	0.67	0.72	0.03
Layer 4	27	1.15	1.37	1.56	0.12	32	0.53	0.63	0.71	0.05
Domen Cave Site										
Horizon V	4	1.27	1.34	1.44	—	7	0.63	0.68	0.72	0.03
Kannondo Cave Site										
Horizon unknown	4	1.28	1.40	1.61	—	4	0.55	0.62	0.65	—
Horizon I	1	—	1.39	—	—	1	—	0.69	—	—
Horizon J	2	1.38	1.39	1.40	—	2	0.68	0.73	0.78	—
Horizon L	1	—	1.63	—	—	1	—	0.75	—	—
LATE PLEISTOCENE (<i>P. cf. smithii</i>)										
Mejiro-do Cave°	3	1.32	1.39	1.45	—	3	0.64	0.65	0.66	—
Suse Quarry (East Fissure)°°	2	1.46	1.47	1.47	—	2	0.64	0.66	0.68	—
Kannondo Cave Site										
Horizon M (upper)	17	1.29	1.46	1.65	0.12	19	0.65	0.70	0.79	0.04
Horizon M (lower)	12	1.30	1.48	1.72	0.14	13	0.57	0.69	0.76	0.05
Horizon N	14	1.20	1.41	1.60	0.11	17	0.53	0.65	0.77	0.06
Horizon O (upper)	11	1.33	1.48	1.71	0.11	17	0.54	0.69	0.78	0.06
Horizon O (lower)	9	1.40	1.55	1.83	0.13	11	0.67	0.75	0.86	0.06
Horizon P	1	—	1.53	—	—	3	0.64	0.71	0.77	—
Yage Quarry										
Site 4	1	—	1.33	—	—	1	—	0.66	—	—

Genus *Microtus* SCHRANK, 1798

Characters

The following characters are found in common in the Japanese fossil and living *Microtus*.

Osteological characters —

The bony palate terminates posteriorly in complicate double shelved structure with a well-developed secondary shelf (Fig. 137), which contrasts with the simple structure seen in *Clethrionomys* and *Phaulomys*. A distinct median ridge on the palate extends posteriorly to form a inclined septum which separates a pair of distinct lateral pits on the secondary shelf.

The mandible is rather heavily built (Figs. 140, 149, 156, 157). The symphyseal eminence is well-developed. Just above this eminence, a strong prominence is present on the lingual face

of the horizontal ramus. The area between the ascending ramus and alveoli of lower molars is wide and deeply pocketed. The alveolus of lower incisor passes the lingual side of M_1 and turns buccally between M_2 and M_3 . Consequently M_3 is displaced, and the capsule for M_3 forms a distinct protuberant area on the lingual face of the horizontal ramus. The capsule for the incisor on the lingual face of the ascending ramus is very distinct and shaft-like. The mandibular foramen opens on the anterior face of the capsule at the base of the condylar process. Its position is more anterior than those of *Clethrionomys* and *Phaulomys*. The posterior end of the incisor forms a distinct prominence on the buccal face of the condylar process. It is much higher than the occlusal surfaces of the lower molars in position. The upper and lower masseteric crests are distinct on the buccal face of the horizontal ramus. The mental foramen is situated below the anterior margin of M_1 or somewhat anterior to that position.

Dental characters —

The molars are rootless. The salient angles are sharply pointed. The re-entrant angles are filled with rich crown-cementum. The thickness of enamel is well differentiated from part to part. Namely, the enamel is generally thicker on the concave side of each triangle than on the convex side. Moreover it remarkably thins off at the bottom of each re-entrant angle. The triangles are well alternating in position. The lingual ones are larger than or equal to the buccal ones in size.

In the upper molars, the anterior wall of the anterior loop is roundly convex. The enamel interrupts at both sides of the anterior loop and the posterior end of the crown. The isthmuses of dentine fields are always closed except Is 5 of M^3 whose width is variable even intraspecifically.

M^1 is composed of an anterior loop and four closed triangles. The postero-lingual extra angle typically found in *Microtus agrestis* is completely absent. M^2 is also composed of an anterior loop and three closed triangles. The extra angle present in *M. agrestis* is also lacking. M^3 is made up of an anterior loop, three triangles, and a posterior loop. The posterior loop is quite variable in shape, and its variation has taxonomical value as discussed in the subsequent sections.

In the lower molars, the posterior wall of the posterior loop is roundly convex. The enamel interrupts on both sides of the posterior loop and the anterior wall of the crown.

M_1 is composed of an anterior loop, four to six closed triangles and a posterior loop. The morphology of the anterior loop and the number of closed triangles are important for specific distinction. M_2 also comprises four closed triangles and a posterior loop. M_3 always carries three closed fields such as a posterior loop, a confluent field of T1 with T2 and that of T3 with T4. Consequently, Is 1 and Is 3 are always closed. The mode of development of BSA3 is variable, but it seems to be less valuable for specific distinction.

From taxonomic viewpoints, it can be stated that the specific distinctions of isolated M^3 and M_1 are possible, but those of isolated M^1 , M^2 , M_2 and M_3 are impossible, because the shapes of the last four molars are uniform interspecifically.

Problems on the classification of the Japanese fossil *Microtus*

Microtus is a distinct group within the Japanese arviculids, and easily distinguishable from others by its palatal and mandibular structures and by its molar patterns. However the specific distinction only by fragmental fossil materials is rather difficult in this genus. Because most of the Japanese fossils are isolated teeth and fragmental mandibles, their classification was quite insufficient until recently.

The first record of fossil *Microtus* in Japan was given by SHIKAMA (1933). He reported the occurrence of *M. montebelli* from the Upper Kuzuu Formation. He also listed this species in his subsequent works on the same formation (SHIKAMA, 1937a, c; 1949). NAORA (1954) also recorded *M. montebelli* from several caves and fissures in the Kuzuu Area and from Matsugae Cave in Kitakyushu. Subsequently, fossils of *Microtus* were reported from other Pleistocene localities by NAKAJIMA and KUWANO (1957), SHIKAMA and OKAFUJI (1958) and HASEGAWA (1966, 1972). In all these works, the fossils are identified as a single species, *M. montebelli*, without exception. However most of these identifications are unreliable, because neither descriptions nor clear illustrations are given except NAORA's work.

In 1972, KANEKO noticed the occurrence of "*M. oeconomus*" (*M. epiratticepoides* of the present author) from Matsugae Cave. Additional occurrence of "*M. oeconomus* (= *ratticeps*)" was reported from the Akiyoshi Area by AIMI (1974). Subsequently, KOWALSKI and HASEGAWA (1976) divided the fossil *Microtus* known from Japan into two species such as *M. montebelli* and *M. epiratticeps*. The latter species is identical with *M. oeconomus* in KANEKO (1972) and AIMI (1974). KOWALSKI and HASEGAWA's classification was followed by the later authors (HASEGAWA *et al.*, 1977; KAWAMURA, 1977a, 1981, 1982; KAWAMURA and KAJIURA 1980 *etc.*).

These previous works are, however, apparently insufficient from the viewpoints of the analysis of variation and the comparison with living and fossil species. Therefore the revision based on numerous fossil and living materials is requested. Because M_1 and M^3 patterns are most important for the specific distinction of the fossil materials as already mentioned, the present author carried out the morphotype analysis and detailed measurements of these molars in order to examine the validity of each character. Although the detailed description will be given in the subsequent sections, the basic problems on the classification of the fossil materials are discussed here.

M_1 —

M_1 pattern is much more important for the palaeontological works of *Microtus* than M^3 pattern, so that many previous palaeontologists described M_1 pattern only. Accordingly, the characters of M_1 pattern are first discussed here.

It is one of key characters for the identification of isolated M_1 whether Is 5 and/or Is 6 are open or closed. Both Is 5 and Is 6 are open in the ancestral groups such as the subgenera *Allophaiomys*, *Phaiomys* and *Pedomys*. In the subgenus *Pitymys*, Is 5 is open, but Is 6 is closed. On the other hand, such species as *Microtus oeconomus* and *M. paroperarius* are characterized by closed Is 5 and open Is 6. In the species such as *M. agrestis*, *M. gregalis*, *M. arvalis* and *M. montebelli*, both Is 5 and Is 6 are closed.

In the Japanese fossil *Microtus* hitherto known, Is 5 is always closed and generally has the same width as those of Is 4, 3, 2 and 1. However the width of Is 6 is variable. Therefore its width against that of Is 5 is taxonomically important. AIMI (1980) proposed the criterion for the living *Clethrionomys* and "*Eothenomys*" whether the isthmuses are open or closed, as already mentioned. However his criterion is not suitable for the present purpose, because the molars of *Microtus* are generally larger than those of *Clethrionomys* and "*Eothenomys*," and the absolute value of the isthmus width varies in accordance with the size of each individual. Thus the present author proposes "isthmus index" here, as the criterion whether Is 6 is open or closed. The minimum width of each isthmus is measured between both inner faces of opposite enamel bands (Fig. 125). The isthmus index is calculated as the ratio of these values by the following formulas:

In case the widths of Is 5, 4, 3 and 2 are constant,
 isthmus index = width of Is 6 / width of Is 5.

This formula is applicable to the most fossil specimens.

In case the widths of Is 5, 4, 3 and 2 are variable,
 isthmus index = width of Is 6 / mean width of Is 5, 4, 3 and 2.

This case is rather rare.

The measurements of hundreds of the living and fossil specimens have revealed that 2.0 of this index is the most important value to distinguish open Is 6 from closed one (Fig. 126).

All the specimens of the living *Microtus montebelli* examined in this study have the isthmus index less than 2.0. On the other hand, the Middle Pleistocene *Microtus* population from Locality 3 of Ube Kosan Quarry can be divided into two groups by this index. One is a "closed" group with the index less than 2.0. Another is an "open" group with the index more than 2.0 (typically more than 3.0). The former group is rare in the lower layers of this locality, but increases upward. In the Late Pleistocene localities, as figured in Fig. 126, these two groups can be recognized, although the latter group is few in number. The latter group is referred to *M. epiratticepoides* sp. nov. in this paper.

The degree of the development of BSA4 is another key character in M_1 of the Japanese

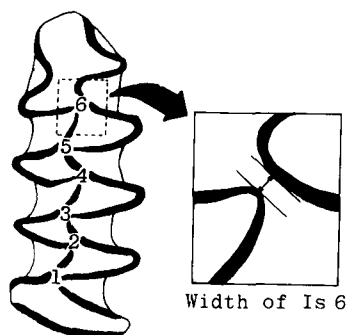


Fig. 125. Method of measurements for the minimum width of each isthmus in M_1 of the Japanese *Microtus*. The width between both inner faces of enamel bands is measured. 1-6, number of isthmus.

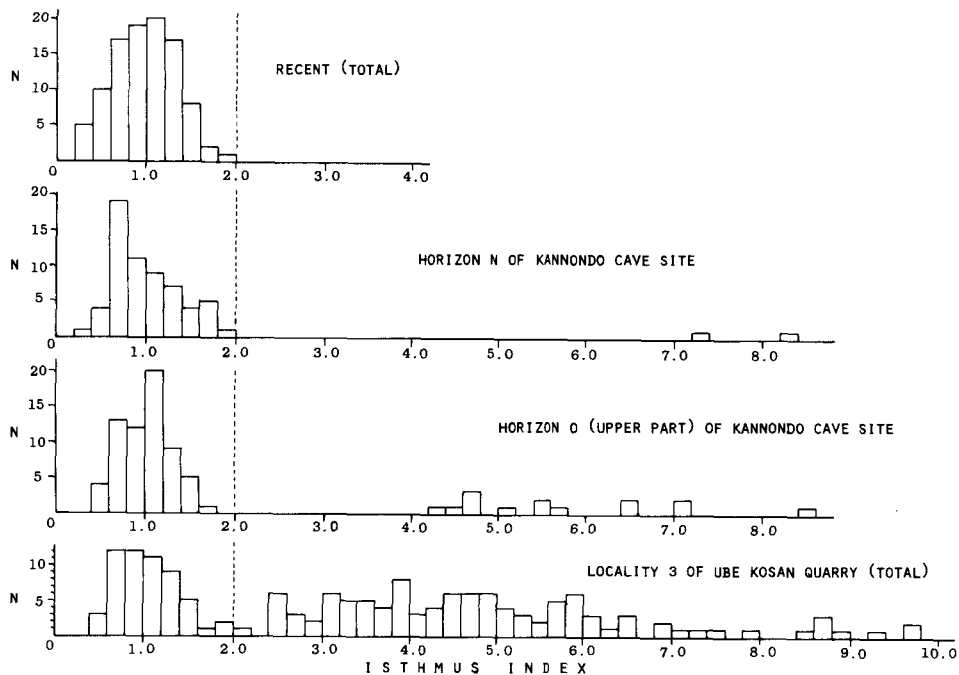


Fig. 126. Histograms of the isthmus index of M_1 in the Japanese *Microtus*. The recent population comprises only one species, *M. montebelli*, where all specimens carry the isthmus index less than 2.0. Others are three representative fossil populations which are composed of more than one species. In these populations, bimodal distributions are given, where both clusters are approximately bordered at 2.0. N, number of specimens.

Microtus. By this character, the former group with closed Is 6 can be subdivided into two forms. Because all the specimens of the living *M. montebelli* carry well-developed BSA4 in M_1 , the fossils with this character are identifiable as *M. montebelli*. In the Pleistocene fossil assemblages, however, the specimens with poorly developed BSA4 or without BSA4 are sometimes observed. Although this form is generally rare, it is not so few in some layers of Locality 3 of Ube Kosan Quarry. Because of the absence of intermediate forms, it can be treated as a separate form from *M. montebelli*, and is assigned to *M. cf. brandtioides* here.

M^3 —

Although the morphology of the anterior part (anterior loop, T2, T3 and T4) is considerably stable, that of the posterior loop is highly variable not only interspecifically but also intraspecifically. Therefore the morphological analyses of the latter part are essential to the classification. The various shapes of the posterior loop can be arranged into a series from a simple type to complicate one (Fig. 127).

In the simplest type, it is only elliptical or sub-triangular, so that LRA4 and LSA5 are undeveloped and LSA4 is not differentiated from the main part of the posterior loop as a distinct projection. When LSA4 becomes the distinct projection, the posterior loop shows

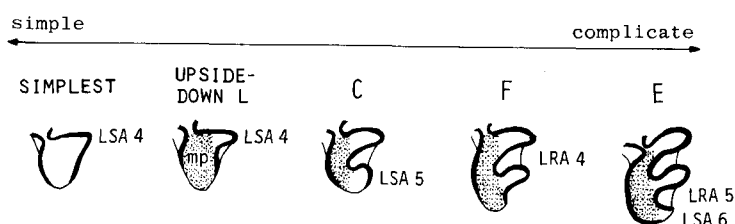


Fig. 127. Morphotypes of the posterior loop of M^3 in the Japanese *Microtus*. A series from a simple type to a complicate one is recognized. mp, main part of the posterior loop. For detailed explanation see text.

upside-down L-shape. Furthermore, as well-defined LRA4 is formed by the development of LSA5, the posterior loop becomes C-shaped. Elongating posteriorly to form shallow LRA5, it shows F-shape. Moreover additional development of LSA6 makes it E-shape, which is the most complicate pattern.

None of the lower tooth row in connection with the upper one has been hitherto found in the Japanese fossil localities examined here. Consequently, it is a difficult problem how to combine the above-mentioned three forms of M_1 with any types of M^3 . A clue to solve this problem is provided by the analyses of M^3 pattern in the living *M. montebelli* and of M^3 assemblages from the Middle Pleistocene localities where M_1 of *M. epiratticepoides* and *M. cf. brandtioides* are exclusively found.

M^3 of the living *M. montebelli* is characterized by the posterior loop with complicate pattern (C-, F- or E-shaped ones). In the Middle Pleistocene localities where M_1 of *M. montebelli* is not found, M^3 with such a complicate posterior loop is absent. All M^3 have the simplified posterior loop which belongs to the upside-down L-shaped or simplest types. These facts indicate that the fossil M^3 with the complicate posterior loop are identifiable as *M. montebelli*, and those with the simplified one are referable to *M. epiratticepoides* or *M. cf. brandtioides*. In those Middle Pleistocene localities, M^3 with the upside-down L-shaped posterior loop are much more abundant than those with the simplest one. As regards M_1 from the same localities, the frequency of *M. epiratticepoides* is generally much higher than that of *M. cf. brandtioides*. Therefore it is most probable that M^3 of *M. epiratticepoides* carries the upside-down L-shaped posterior loop, and that of *M. cf. brandtioides* has the simplest one. Such an assumption is supported by the description of the Chinese *M. brandtioides* in which M_1 with similar pattern to the Japanese counterpart is exactly combined with the simplest M^3 .

The distinction between the C-shaped posterior loop and upside-down L-shaped one is of great importance for the distinction between *M. montebelli* and *M. epiratticepoides*. The C-shaped one generally has a slender main part and well-developed LSA5. However the upside-down L-shaped one carries a broader main part usually without LSA5, and sometimes with faint LSA5. Although there seem to be some intermediate forms, these two types are separable by the following measurements:

1. Length of LSA4 (LS_4 in Fig. 128)
2. Length of LSA5 (LS_5 in Fig. 128)

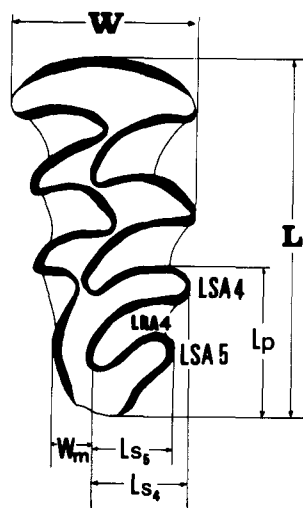


Fig. 128. Method of the detailed measurements of M^3 in the Japanese *Microtus*.

L, length of the occlusal surface; W, width of the occlusal surface; Lp, length of the posterior loop; Ls₄, length of LSA4; Ls₅, length of LSA5; Wm, width of the main part of the posterior loop.

3. Width of the main part (Wm in Fig. 128)

The ratios (Ls_5/Ls_4 and Wm/Ls_4) are calculated for all the examined specimens (e.g. Fig. 129). The relationship between these ratios is shown in the scatter diagrams (Figs. 130–132). Almost all the specimens of the living *M. montebelli* take Ls_5/Ls_4 more than 0.5, but Wm/Ls_4 less than 1.0. In M^3 of *M. epiratticepoides* from the Middle and Late Pleistocene localities, Ls_5/Ls_4 is mostly less than 0.45, and Wm/Ls_4 more than 1.0. Therefore 0.45 of Ls_5/Ls_4 and 1.0 of Wm/Ls_4 can be regarded as the approximate boundary between these two species. Because LRA4 is undeveloped in the simplest type, Ls_4 , Ls_5 and Wm are not measurable for *M. cf. brandtioides*.

Key to the species of the Japanese *Microtus*

Most of the fossil specimens are isolated molars. Thus it is convenient to give keys separately to M^3 and M_1 .

Key to M^3 —

1. Posterior loop complicate, namely C- or F-shaped; LSA5 well developed; Ls_5/Ls_4 more than 0.45; Wm/Ls_4 mostly less than 1.0. *M. montebelli*
- Posterior loop simple; LSA5 weak or absent. 2
2. Posterior loop mostly upside-down L-shaped, and sometimes simple C-shaped; Ls_5/Ls_4 ranging from 0 to 0.45; Wm/Ls_4 mostly more than 1.0. *M. epiratticepoides*, sp. nov.
- Posterior loop very simple; LSA4 remarkably short or indistinctly projected from the main part; LRA4 absent so that Ls_4 , Ls_5 and Wm are not measurable. *M. cf. brandtioides*

Key to M_1 —

1. With four closed triangles; isthmus index more than 2.0 (mostly more than 3.0); BSA4 variable. *M. epiratticepoides*, sp. nov.
- With more than four closed triangles; isthmus index less than 2.0. 2
2. With five or six closed triangles; both BSA4 and BRA4 well-developed. *M. montebelli*
- With five closed triangles; BSA4 absent or less developed; BRA4 always absent. *M. cf. brandtioides*

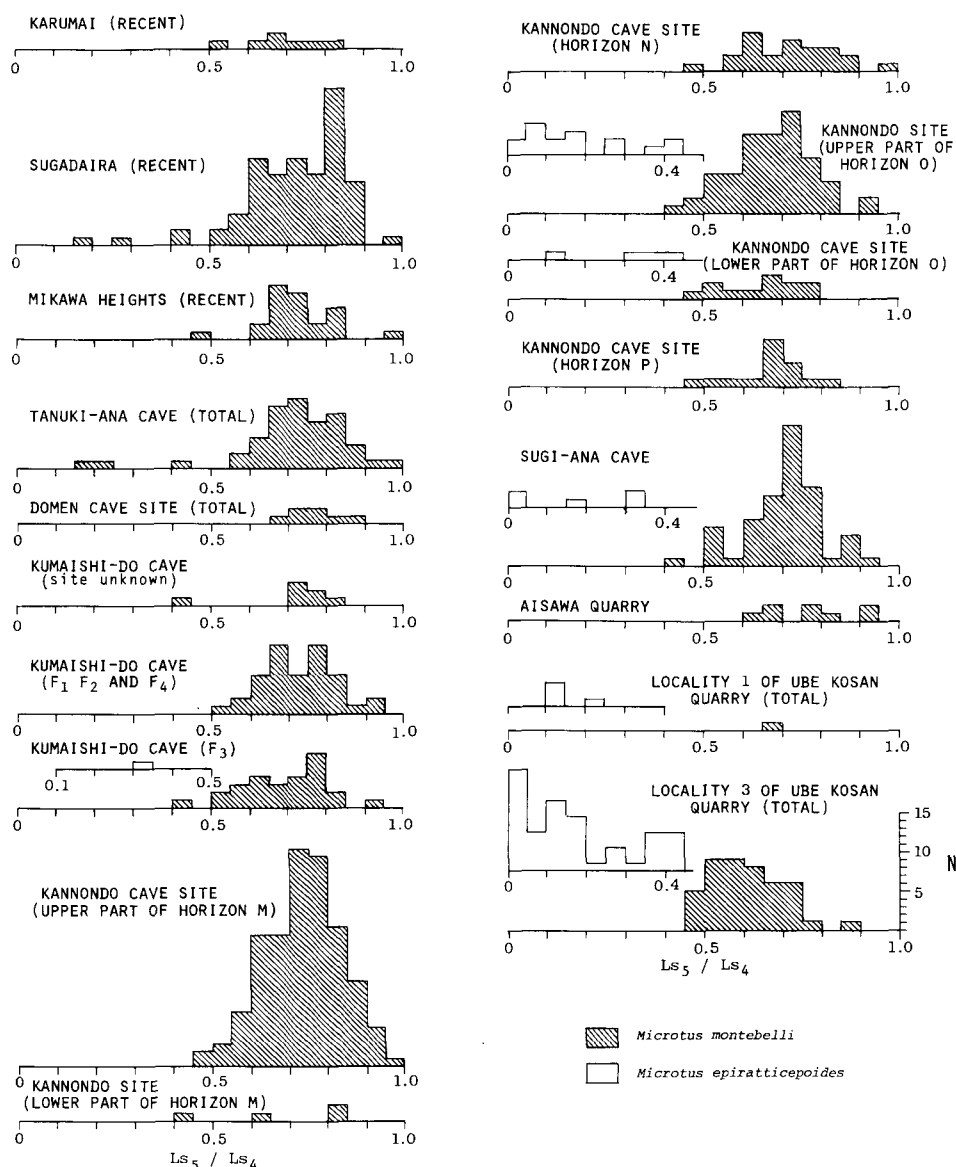


Fig. 129. Histograms of Ls_5/Ls_4 in the recent and fossil M^3 assemblages of the Japanese *Microtus*.

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

The Early Pleistocene records of *Microtus* are very few in East Asia (Fig. 133, Table 60). All of them are possibly dated as the late Early Pleistocene. *Arvicola terraerubrae* TEILHARD from Huaiyu (Locality 18) near Peking is similar to *Microtus* (*Allophaiomys*) *pliocaenicus* in molar pattern and size. The genus *Arvicola* is much larger in size and considered to have evolved

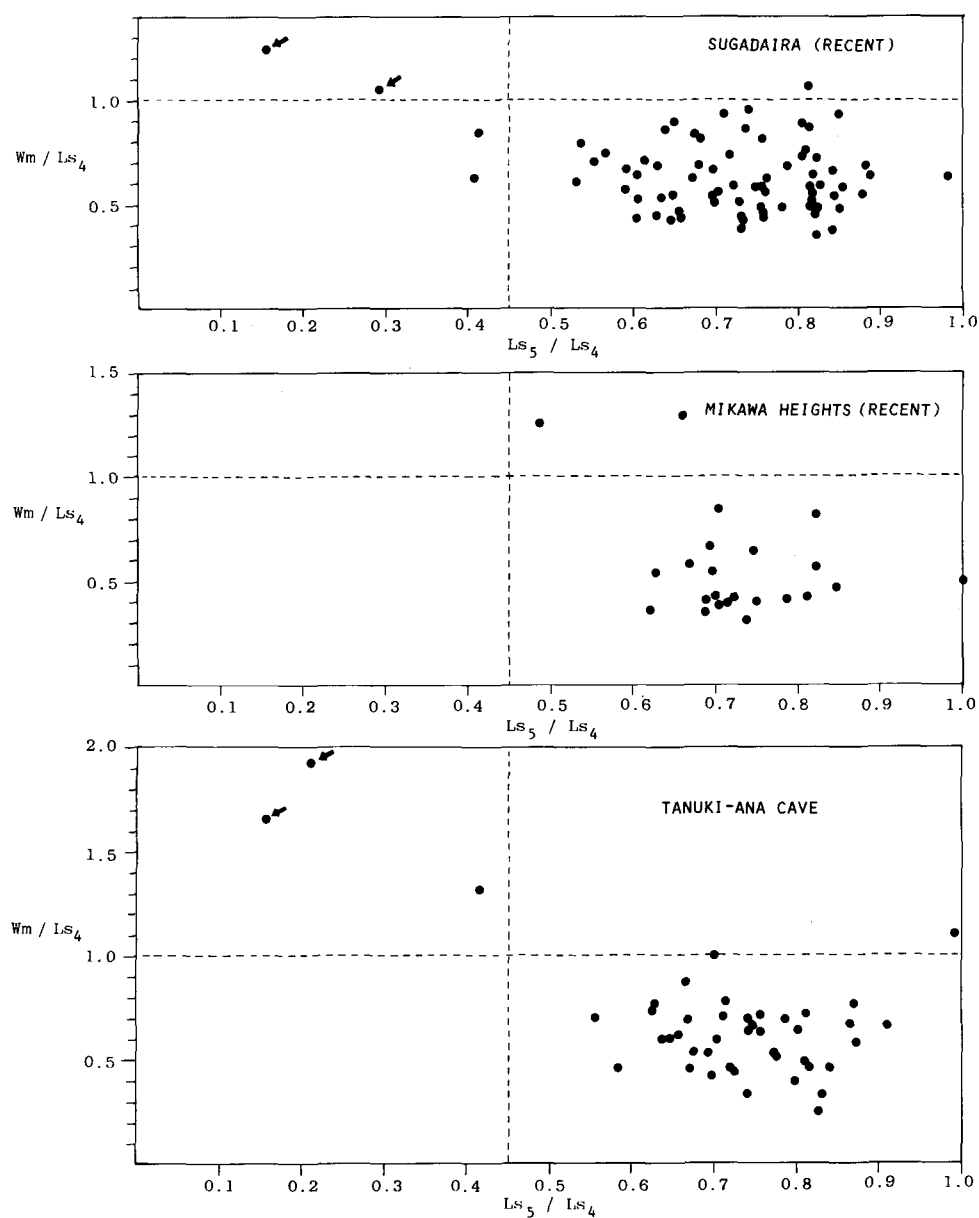


Fig. 130. Relationship between Ls_5/Ls_4 and Wm/Ls_4 in the recent and Holocene M^3 assemblages of the Japanese *Microtus*. All the specimens are identified as *M. montebelli*. Arrow indicates abnormal individual.

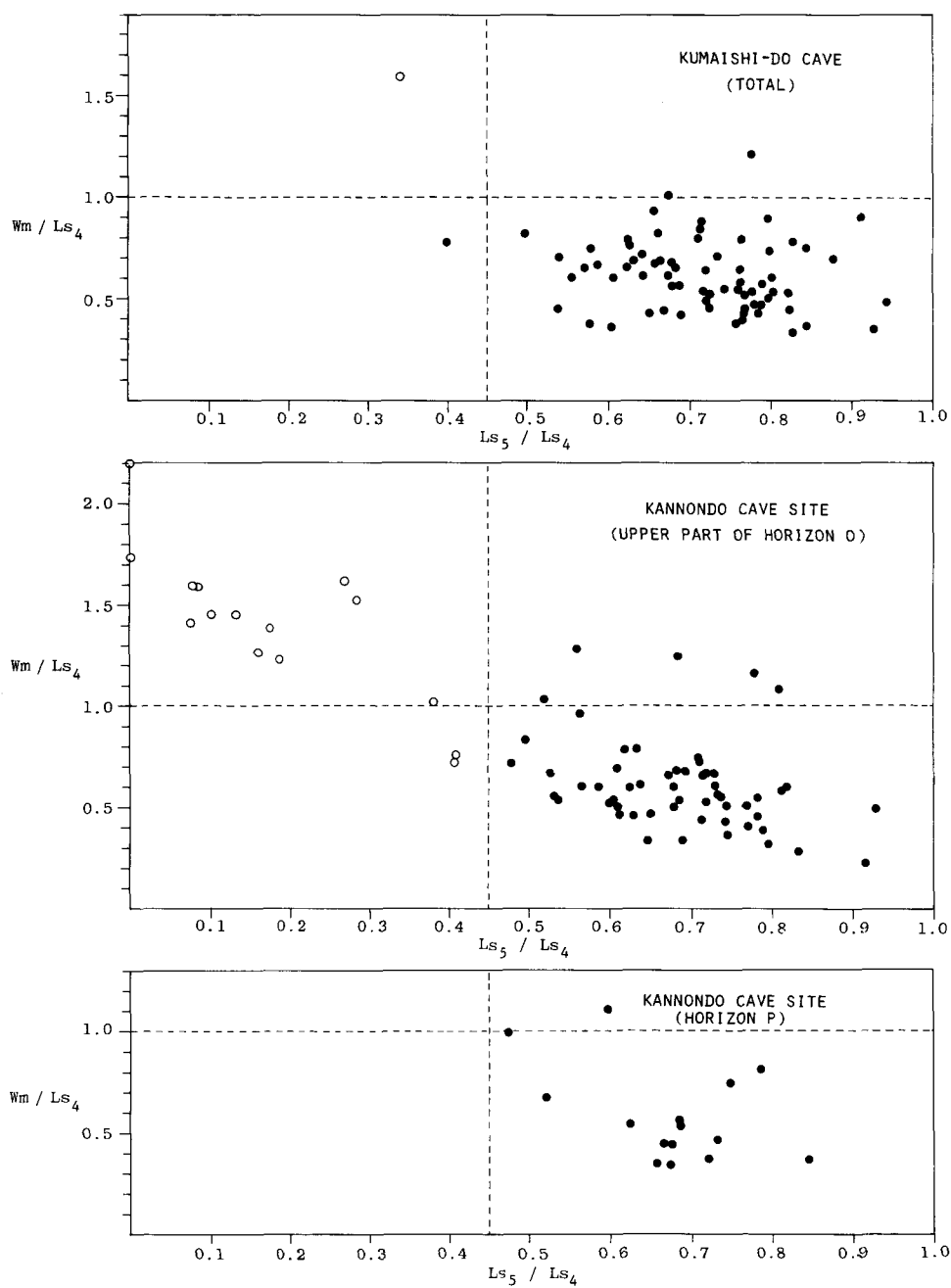


Fig. 131. Relationship between Ls_5/Ls_4 and Wm/Ls_4 in the Late Pleistocene M^3 assemblages of the Japanese *Microtus*. Solid circle, *M. montebelli*; open circle, *M. epiratticepoides*.

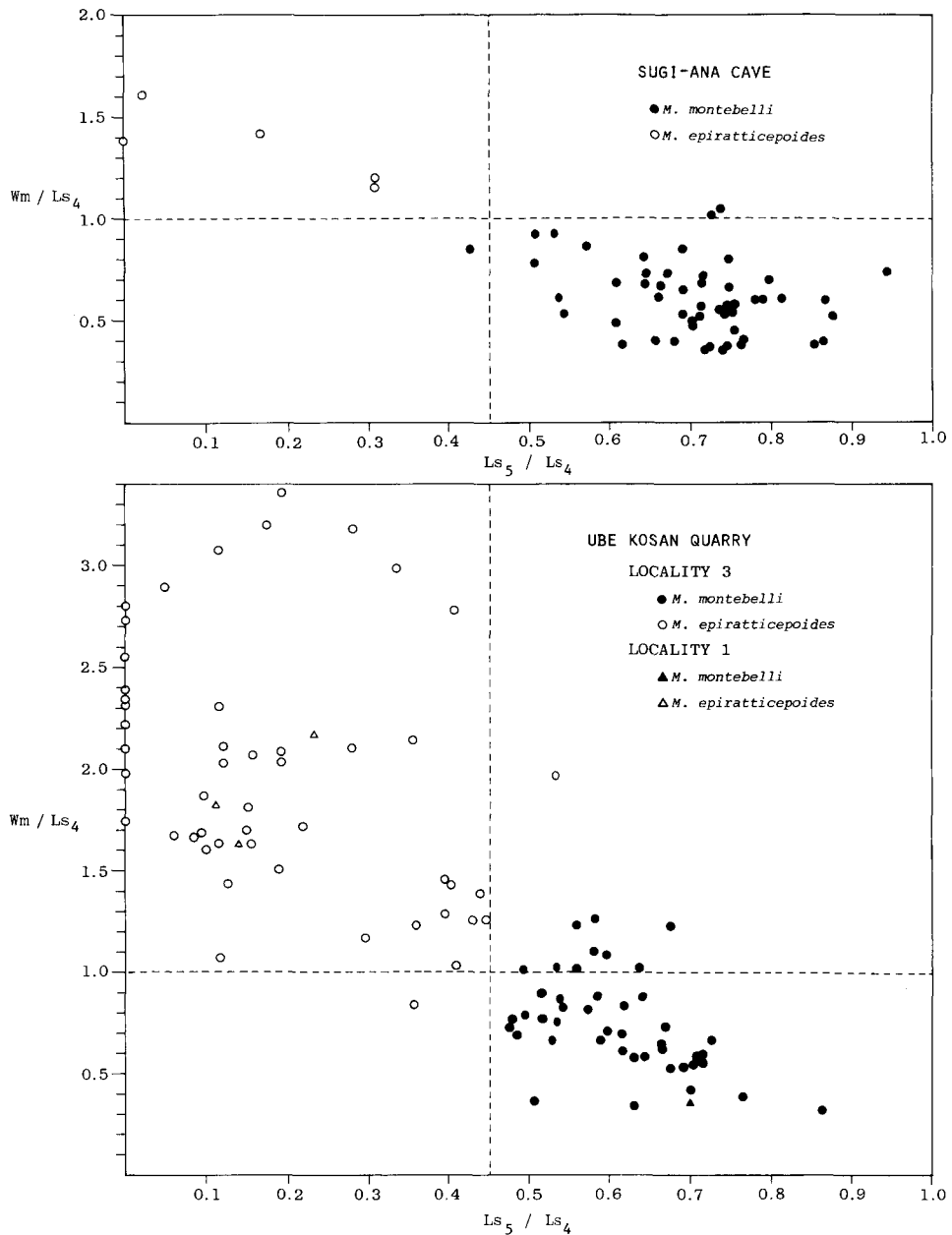


Fig. 132. Relationship between Ls_5/Ls_4 and Wm/Ls_4 in the Late and Middle Pleistocene M^3 assemblages of the Japanese *Microtus*. Solid circle and triangle, *M. montebelli*; open circle and triangle, *M. epiratticepoides*.

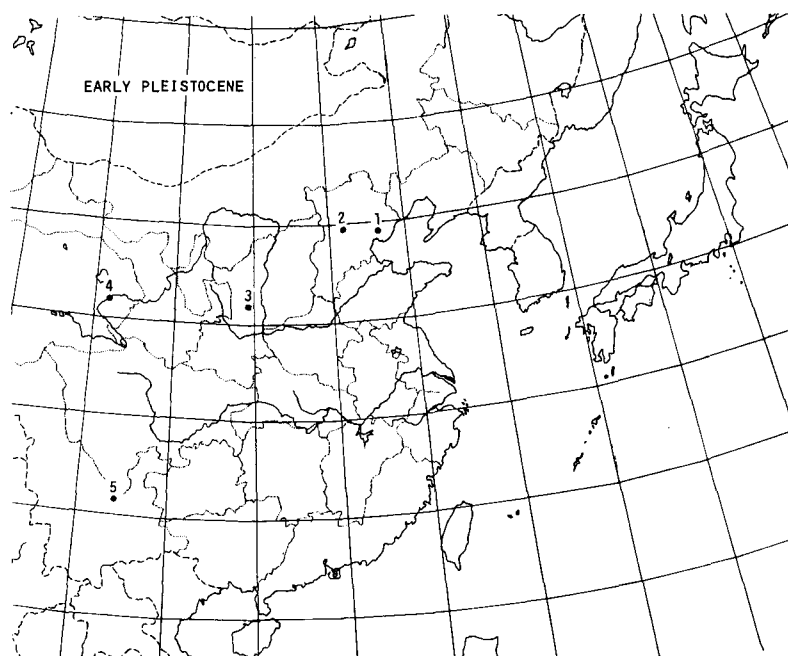


Fig. 133. Early Pleistocene fossil localities of *Microtus* in East Asia. 1, Chiachiashan; 2, Huaiyu; 3, Luochuan; 4, Gonghe Basin; 5, Yuanmou Basin. For detailed explanation see Table 60.

directly from *Mimomys* in the Middle Pleistocene of Europe. Therefore such generic allocation is quite doubtful. The present author provisionally includes "*terraerubrae*" in *Allophaiomys*, if this form has rootless molars as described by TEILHARD (1940)*. In addition to this form, *Microtus* sp. is recorded from Yuanmou Basin, Luochuan and Chiachiashan, and *M. brandtioides* is found in Gonghe Basin.

The Middle Pleistocene records of *Microtus* are abundantly known from North China, Korea and Japan (Fig. 134, Table 61). The Chinese species are represented by *M. epiratticeps* YOUNG, *M. brandtioides* YOUNG and *M. complicidens* PEI. Their distribution is restricted to the north of the Yangtze River. These species are possibly the descendants of the *Allophaiomys*-like ancestor of the Early Pleistocene. However the relationship between the Early and Middle Pleistocene forms has not been studied owing to the scarcity of the Early Pleistocene records. The comparative studies with the evolutionary trends of *Microtus* established in Europe are requested in the Chinese materials.

From the Middle Pleistocene sediments of Localities 1, 3 and 9 of Choukoutien, *Pitymys*

* The records of "*Arvicola terrae-rubrae*" are not uncommon, but some of them are not similar to *Allophaiomys* in molar pattern, or carry rooted molars. Unfortunately, the present author could not observe the type specimens of this species at the Institute of Vertebrate Palaeontology and Palaeoanthropology in Peking. According to ZHENG and LI (1986), they are not stored there.

Table 60. Early Pleistocene fossil localities of *Microtus* in East Asia. The numbers on the left side correspond to those in Fig. 133.

LOCALITY	IDENTIFICATION (PARTLY REVISED)	REFERENCES	REMARKS
CHINA			
1. Chiachiashan	<i>Microtus</i> sp.	Pei (1930), Kowalski & Li (1963)	No descriptions are given.
2. Huaiyu (Locality 18)	<i>M. (Allophaiomys) terraerubrae</i>	Teilhard (1940)	Teilhard originally assigned this form to <i>Arvicola terraerubrae</i> , but it is tentatively included in <i>Allophaiomys</i>
3. Luochuan	<i>Microtus</i> sp.	Kawamura & Xue (1984)	No descriptions are given.
4. Gonghe Basin	<i>M. brandtioides</i>	Zheng et al. (1985)	
5. Member IV (Shang-nabang Formation) in Yuanmou Basin	<i>Microtus</i> sp.	Ji & Li (1979), Li (1981), Liu & Ding (1983)	No descriptions are given. Liu & Ding considered the age of Member IV as the early Middle Pleistocene

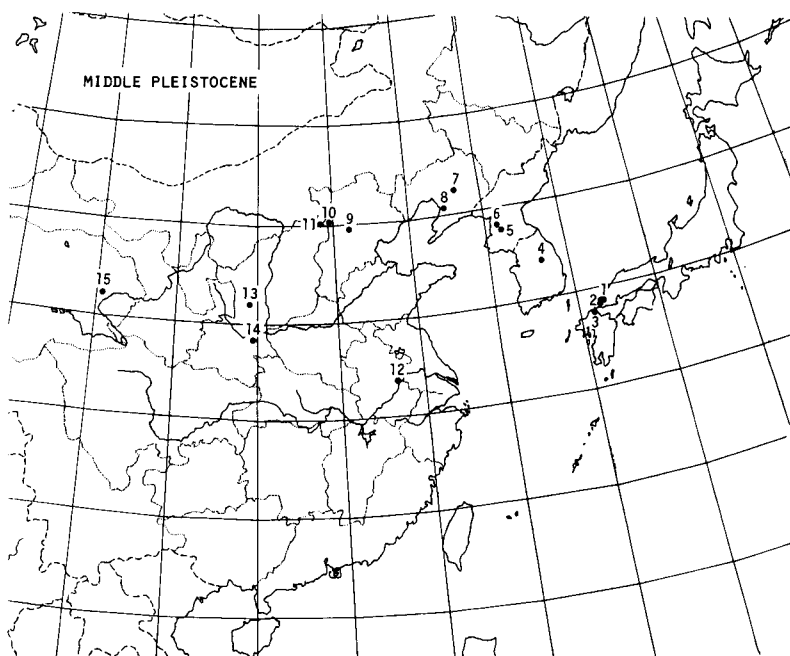


Fig. 134. Middle Pleistocene fossil localities of *Microtus* in East Asia. 1, Ikumo Quarry; 2, Akiyoshi Area (Ando Quarry, Tokuyama Soda Quarry, and Localities 1, 3 and 4 of Ube Kosan Quarry); 3, Matsugae Cave; 4, Chommal Yonggul Cave; 5, Sangwon Komunmoru Cave; 6, Cheon-dong Site; 7, Anping; 8, Jinniushan; 9, Choukoutien (Localities 1, 2, 3, 5, 9 and 15); 10, Nihewan Area; 11, Hsuchiayao; 12, Hexian; 13, Luochuan; 14, Gongwangling (Lantian); 15, Gonghe Basin. For detailed explanation see Table 61.

Table 61. Middle Pleistocene fossil localities of *Microtus* in East Asia. The numbers on the left side correspond to those in Fig. 134.

LOCALITY	IDENTIFICATION (PARTLY REVISED)	REFERENCES	REMARKS
JAPAN			
1. Ikumo Quarry	<i>M. epiratticepoides</i> <i>M. cf. brandtioides</i>	Hasegawa (1963, 1966); Kowalski & Hasegawa (1976)	Originally assigned to <i>M. montebelli</i> or <i>M. epiratticeps</i>
2. Ando Quarry	<i>M. epiratticepoides</i> <i>M. cf. brandtioides</i>	Hasegawa (1966, 1972); Kowalski & Hasegawa (1976); Hasegawa et al. (1977)	Ditto.
2. Tokuyama Soda Quarry	? <i>M. montebelli</i>	Shikama & Okafuji (1958)	No descriptions are given.
2. Locality 3 of Ube Kosan Quarry	<i>M. epiratticepoides</i> <i>M. cf. brandtioides</i> <i>M. montebelli</i>	This paper	
2. Locality 1 of Ube Kosan Quarry	<i>M. epiratticepoides</i> <i>M. montebelli</i>	This paper	
2. Locality 4 of Ube Kosan Quarry	<i>M. epiratticepoides</i>	This paper	
3. Matsugae Cave at Tsunemi	<i>M. epiratticepoides</i>	Naora (1944, 1954); Kaneko (1972); Kowalski & Hasegawa (1976)	Originally assigned to <i>M. montebelli</i> , <i>M. ratticeps</i> or <i>M. epiratticeps</i> .
KOREA			
4. Chommal Yonggul Cave	<i>M. epiratticeps</i> <i>M. brandtioides</i> <i>M. brandti</i> , <i>M. sp.</i>	Sohn (1984)	No descriptions are given.
5. Sangwon Komunmoru Cave	<i>M. epiratticeps</i> <i>M. sangwonensis</i> <i>M. brandti</i> <i>M. fortis</i> , <i>M. sp.</i>	Kim & Kim (1974)	
6. Cheon-dong Site	<i>M. ratticeps</i> <i>M. brandti</i> <i>M. fortis</i>	Kim et al. (1985)	
CHINA			
7. Anping	<i>M. epiratticeps</i>	Zhang et al. (1980)	No descriptions are given.
8. Jinniushan	<i>M. epiratticeps</i>	Archaeological United Team (1976, 1978)	Ditto
9. Locality 1 of Choukoutien	<i>M. epiratticeps</i> <i>M. brandtioides</i>	Zdansky (1928); Young (1934); Chao & Li (1960); Kahlke & Chow (1961)	
9. Locality 2 of Choukoutien	<i>M. brandtioides</i>	Young (1927, 1932, 1934)	
9. Locality 3 of Choukoutien	<i>M. epiratticeps</i> <i>M. brandtioides</i> <i>M. complicidens</i>	Pei (1936)	
9. Locality 5 of Choukoutien	<i>M. epiratticeps</i> <i>M. brandtioides</i>	Pei (1931); Young (1934)	Pei originally assigned them to <i>M. cf. brandti</i>
9. Locality 9 of Choukoutien	<i>cf. M. epiratticeps</i> <i>cf. M. brandtioides</i>	Teilhard (1936)	
9. Locality 13 of Choukoutien	<i>M. cf. brandtioides</i>	Teilhard & Pei (1941)	
10. Nihewan Area	<i>M. brandtioides</i>	Zheng (1981)	
11. Hsuchiayao	<i>M. brandtioides</i>	Chia et al. (1979)	
12. Hexian	<i>M. brandtioides</i>	Huang et al. (1982); Zhang (1983)	
13. Luo-chuan	<i>M. brandtioides</i>	Liu & Yuan (1982); Kawamura & Xue (1984)	
14. Gongwangling	? <i>M. (Allophaiomys) terraerubrae</i>	Hu & Qi (1978)	As regards <i>M. (Allophaiomys) terraerubrae</i> , Hu & Qi did not describe whether the roots of the molars were formed or not.
15. Gonghe Basin	<i>M. epiratticeps</i> <i>M. brandtioides</i>	Zheng et al. (1985)	

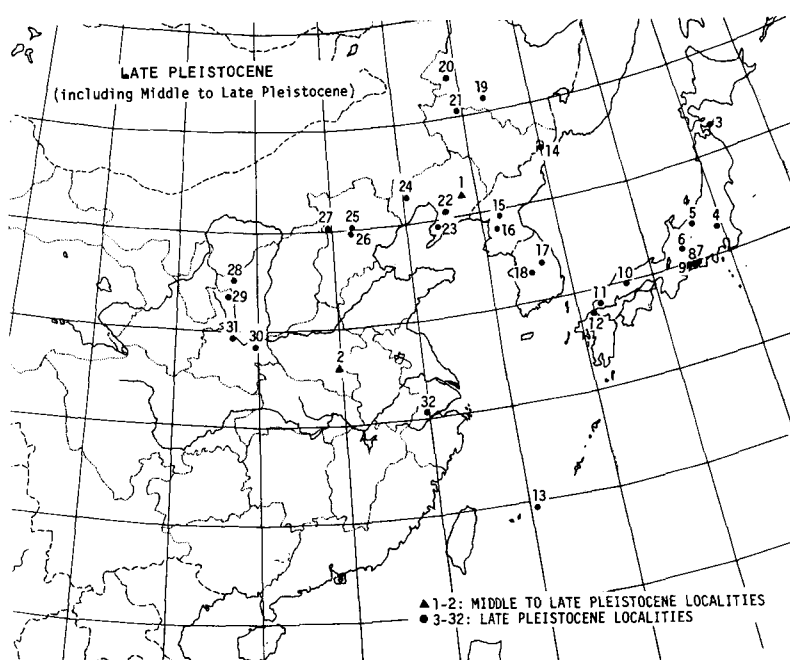


Fig. 135. Late Pleistocene fossil localities of *Microtus* in East Asia (including Middle to Late Pleistocene localities). 1, Miaohoushan; 2, Hsintsai; 3, Shiriya Quarry; 4, Kuzuü Area (Mizunoki Cave, Kadosawa, Miyata First Cave, Miyata Second Cave, Aisawa, Yoshizawa Sekkai no. 8 Quarry, Tuidi, Komagata Sekkai Quarry, Maegawara Cave, Takanosuzawa Cave and Okada Quarry); 5, Lake Nojiri; 6, Sugi-ana Cave and Kumaishi-do Cave; 7, Shiraiwa Mine and Yage Quarry; 8, Tadaki Quarry; 9, Ushikawa Mine and Suse Quarry; 10, Kannondo Cave Site; 11, Akiyoshi Area (Locality 2 of Ube Kosan Quarry and "Ube Kosan Quarry" by SHIKAMA and OKAFUJI, 1958); 12, Seiryukutsu Cave; 13, Pinza-Abu Cave; 14, Dokantin; 15, Tokchon Cave; 16, Mandal-ri Cave Site; 17, Chommal Yonggul Cave; 18, Turubong Cave; 19, Ku-hsiang-tung; 20, Daxingtum; 21, Qingshantou; 22, Xiaogushan; 23, Gulongshan; 24, Gezidong; 25, Longgudong Cave; 26, Upper Cave of Choukoutien; 27, Hutouliang; 28, Sjara-osso-gol; 29, Maoyuan; 30, Laochihe; 31, Qianxian; 32, Fenghuangshan. For detailed explanation see Table 62.

simplicidens Young and *Phaiomys* sp. were described by YOUNG (1934), PEI (1940) and TEILHARD (1936), although their occurrences are very rare. *Pitymys* and *Phaiomys* are usually treated as the subgenera of *Microtus*. However these Choukoutien forms do not show the typical molar pattern of *Microtus*. Moreover, recent Russian authors regard "*P. simplicidens*" as the species of *Eolagulus* (VANGENGIM *et al.*, 1966; AGADJANIAN and ERBAJEVA, 1983 etc.). Therefore these two forms are excluded from the present discussion.

In the Middle Pleistocene of Japan, three species such as *M. epiratticepoides*, *M. cf. brandtioides* and *M. montebelli* are recognized from several localities in west Honshu and Kyushu. *M. epiratticepoides* is closely related to *M. epiratticeps* of China, and probably derived from the ancestor common to the latter species in the continent. *M. cf. brandtioides* is also the allied form to *M. brandtioides* of China. On the other hand, *M. montebelli* appeared in Japan in the later

Table 62. Middle to Late Pleistocene and Late Pleistocene fossil localities of *Microtus* in East Asia. The numbers on the left side correspond to those in Fig. 135.

LOCALITY	IDENTIFICATION (PARTLY REVISED)	REFERENCES	REMARKS
<u>MIDDLE TO LATE PLEISTOCENE</u>			
CHINA			
1. Miaohoushan	<i>M. epiratticeps</i> <i>M. brandtioides</i>	Zhang (1981); Zhang et al. (1984)	No descriptions are given.
2. Hsintsai	<i>M. epiratticeps</i>	Pei (1956)	
<u>LATE PLEISTOCENE</u>			
JAPAN			
3. Shiriya Quarry	<i>M. montebelli</i> ? <i>M. epiratticepoides</i>	Nakajima & Kuwano (1957); Hasegawa (1972); Kowalski & Hasegawa (1976)	Originally assigned to <i>M. montebelli</i> and <i>M. epiratticeps</i> .
4. Mizunoki Cave	? <i>M. montebelli</i>	Naora (1954)	Geological age uncertain and no descriptions.
4. Kadosawa (Kimura Quarry)	? <i>M. montebelli</i>	Shikama (1949)	No descriptions are given.
4. Miyata First Cave	<i>M. montebelli</i>	Shikama (1937b, 1949); Ko- walski & Hasegawa (1976)	No descriptions are given.
4. Miyata Second Cave	<i>M. montebelli</i>	Shikama (1937b, 1949); Ko- walski & Hasegawa (1976)	
4. Aisawa	<i>M. montebelli</i>	Kowalski & Hasegawa (1976); this paper	No descriptions are given.
4. Yoshizawa Sekkai no.8 Quarry	<i>M. montebelli</i>	Kowalski & Hasegawa (1976)	
4. Tuidi	? <i>M. montebelli</i>	Shikama (1937b, 1949)	No descriptions are given.
4. Komagata Sekkai Quarry	? <i>M. montebelli</i>	Naora (1954)	Ditto. Geological age un- certain.
4. Maegawara Cave	? <i>M. montebelli</i>	Naora (1954)	No descriptions are given.
4. Takanosuzawa Cave	<i>M. montebelli</i>	Naora (1954); Kowalski & Hasegawa (1976)	No descriptions are given.
4. Okada Quarry (=Izu- rugahara Cave)	<i>M. montebelli</i>	Shikama (1937b, 1949); Naora (1954)	
5. Lake Nojiri (Noji- ri-ko)	<i>Microtus</i> sp.	Kawamura & Fossil Mammal Research Group of Nojiri- ko Excavation (1979)	Originally assigned to <i>M. montebelli</i> and <i>M. epiratticeps</i>
6. Sugi-ana Cave	<i>M. montebelli</i> <i>M. epiratticepoides</i> <i>M. cf. brandtioides</i>	Kawamura & Kajiura (1980); this paper	
6. Kumaishi-do Cave	<i>M. montebelli</i> <i>M. epiratticepoides</i> <i>M. cf. brandtioides</i>	Kawamura & Ishida (1976); Kawamura (1977); Okumura et al. (1982); this paper	Originally assigned to <i>M. montebelli</i> and <i>M. epiratticeps</i>
7. Shiraiwa Mine	<i>M. montebelli</i> <i>M. epiratticepoides</i> <i>M. cf. brandtioides</i>	Hasegawa (1966); Kowalski & Hasegawa (1976)	
7. Yage Quarry	<i>M. montebelli</i> <i>M. epiratticepoides</i> <i>M. cf. brandtioides</i>	Tomida (1978); this paper	Originally assigned to <i>M. montebelli</i> and <i>M. epiratticeps</i>
8. Tadaki Quarry	<i>M. montebelli</i>	Takai (1962)	
9. Ushikawa Mine	<i>M. montebelli</i>	Suzuki & Takai (1959); Hasegawa (1966); Kowalski & Hasegawa (1976)	Originally assigned to <i>M. montebelli</i> and <i>M. epiratticeps</i>
9. Suse Quarry (East Fissure)	<i>M. montebelli</i>	This paper	
10. Kannondo Cave Site (Horizons M to P)	<i>M. montebelli</i> <i>M. epiratticepoides</i> <i>M. cf. brandtioides</i>	Kawamura (1980, 1981, 1982); Kawamura et al. (1986); this paper	Originally assigned to <i>M. montebelli</i> and <i>M. epiratticeps</i>
11. Locality 2 of Ube Kosan Quarry	<i>M. epiratticepoides</i>	This paper	

Table 62. (Continued)

LOCALITY	IDENTIFICATION (PARTLY REVISED)	REFERENCES	REMARKS
11. Ube Kosan Quarry	? <i>M. montebelli</i>	Shikama & Okafuji (1958)	No descriptions are given. Different fissures or caves from Loc.1 to 4 of the present author.
12. Seiryukutsu Cave	<i>M. montebelli</i>	Kawamura & Sotsuka (1984); this paper	
13. Pinza-Abu Cave	<i>M. oeconomus</i> <i>M. fortis</i> <i>M. sp.</i>	Kaneko (1985)	
KOREA			
14. Dokantin	<i>M. maekawai</i>	Tokunaga & Mori (1939)	Similar species to <i>M. oeconomus</i> or <i>M. epiratticeps</i> .
15. Tokchon (Sungnisan Cave Site)	<i>Microtus sp.</i>	Laboratory of Natural History, Institute of Archaeology (1978)	
16. Mandal-ri Cave Site	<i>Microtus sp.</i>	Kim et al. (1985)	
17. Chommal Yonggul Cave	<i>M. epiratticeps</i> <i>M. brandtioides</i> <i>M. brandti</i> <i>M. fortis</i> , <i>M. sp.</i>	Sohn (1984)	No descriptions are given.
18. Turubong Cave	<i>M. brandtioides</i> <i>M. mandarinus</i> <i>M. fortis</i> , <i>M. sp.</i>	Lee (1983); Sohn (1984)	Ditto.
CHINA			
19. Ku-hsiang-tung	<i>M. cf. oeconomus</i> <i>M. cf. fortis</i> <i>M. brandti</i> <i>M. obscurus</i> <i>M. cf. mongolicus</i> <i>M. gregalis</i>	Tokunaga & Naora (1934, 1939); Tokuda (1939)	Tokuda used " <i>ratticeps</i> " and " <i>pelliceus</i> " instead of " <i>oeconomus</i> " and " <i>fortis</i> " respectively.
20. Daxingtum (near Angangxi)	<i>M. epiratticeps</i>	Huang et al. (1984)	No descriptions are given.
21. Qingshantou	<i>M. brandti</i>	Jin et al. (1984)	
22. Xiaogushan Site	<i>M. epiratticeps</i>	Zhang et al. (1984)	No descriptions are given.
23. Gulongshan	<i>Microtus sp.</i>	Zhou et al. (1984)	Ditto.
24. Gezidong Cave	<i>M. epiratticeps</i>	Archaeological Team of Provincial Museum of Liaoning & IVPP (1975)	
25. Longgudong Cave at Changping	<i>M. epiratticeps</i> <i>M. brandtioides</i>	Huang (1981)	No descriptions are given.
26. Upper Cave of Choukoutien	<i>M. cf. epiratticeps</i> <i>M. cf. brandtioides</i> (Besides these, more than one species are possibly present)	Pei (1940)	Originally, Pei did not give definite taxonomic positions to them, and referred to " <i>M. epiratticeps</i> (<i>M. brandtioides</i>)".
27. Hutouliang	<i>M. brandtioides</i>	Gai & Wei (1977)	No descriptions are given.
28. Sjara-osso-gol	<i>M. cf. oeconomus</i> <i>M. brandtioides</i>	Boule et al. (1928); Young (1934)	Boule et al. originally assigned <i>M. brandtioides</i> to <i>Microtus sp.</i>
29. Maoyuan	<i>M. complicidens</i>	Zhao et al. (1986)	No descriptions are given.
30. Laochihe at Lantian	<i>M. brandtioides</i>	Zhang et al. (1978)	Ditto.
31. Qianxian	<i>Microtus sp.</i>	Qiu (1984)	Ditto.
32. Fenghuangshan	<i>M. brandtioides</i>	Han & Zhang (1978)	Ditto.



Fig. 136. Holocene fossil localities of *Microtus* in East Asia. 1, Numazu Shellmound; 2, Tochibara Rockshelter Site; 3, Same Cave; 4, Kitoragawa Site; 5, Taishaku Area (Kannondo Cave Site, Domen Cave Site and Anagami Rockshelter Site); 6, Akiyoshi Area (Tanuki-ana Cave, Husen-ana Cave, Makurazino-ana Cave, Koziki-ana Cave and Irimino-ana Cave); 7, Hirao-dai Area (Ohera-ana Cave and Ojika-do Cave). For detailed explanation see Table 63.

period of the Middle Pleistocene. This species is rather similar to *M. arvalis* of Europe and *M. maximowiczii* of Transbaikalia. It might migrate from Siberia via Northeast China and the Korean Peninsula.

The Late Pleistocene *Microtus* is also abundantly found in a number of localities in North China (Fig. 135, Table 62). In addition to *M. epiratticeps* and *M. brandtioides*, several species are recorded from some localities; namely *M. cf. pelliceus*, *M. obscurus*, *M. cf. mongolicus* and *M. gregalis* from Ku-hsiang-tung (TOKUDA, 1939), and *M. maekawai* from Dokantin (a similar form to *M. oeconomus*; TOKUNAGA and MORI, 1939). Moreover the present author supposes that the *Microtus* assemblage in the Upper Cave of Choukoutien appears to comprise more than three species (including *M. epiratticeps* and *M. brandtioides*), although the definite specific names were not given by PEI (1940). Because six or seven species are distributed in the present North China, it is rather reasonable that various species were existent in the Late Pleistocene.

The Late Pleistocene and Holocene records of *Microtus* are considerably abundant in Japan (Figs. 135, 136; Tables 62, 63). The same species as those of the Middle Pleistocene (*M. epiratticepoides*, *M. cf. brandtioides* and *M. montebelli*) are known from the Late Pleistocene localities, where *M. montebelli* remarkably predominates over other two species. In the

Table 63. Holocene fossil localities of *Microtus* in East Asia. The numbers on the left side correspond to those in Fig. 136.

LOCALITY	IDENTIFICATION	REFERENCES	REMARKS
JAPAN			
1. Numazu Shell-mound	? <i>M. montebelli</i>	Naora (1944)	No descriptions are given.
2. Tochibara Rock-shelter Site	? <i>M. montebelli</i>	Miyao et al.(1980)	Ditto.
3. Same Cave	? <i>M. montebelli</i>	Naora (1944); Shikama et al.(1952)	Ditto.
4. Kitoragawa Site	<i>M. montebelli</i>	This paper	
5. Kannondo Cave Site (Horizons A to L)	<i>M. montebelli</i>	Kawamura (1978, 1979); this paper	
5. Domen Cave Site	<i>M. montebelli</i>	This paper	
5. Anagami Rock-shelter Site	<i>M. montebelli</i>	Kawamura (1983); this paper	
6. Tanuki-ana Cave	<i>M. montebelli</i>	Kawamura & Tamiya (1980); this paper	
6. Husen-ana Cave	<i>M. montebelli</i>	This paper	
6. Makurazino-ana Cave	<i>M. montebelli</i>	Shikama & Okafuji (1958); Kowalski & Hasegawa (1976)	
6. Koziki-ana Cave	? <i>M. montebelli</i>	Shikama & Okafuji (1958)	No descriptions are given.
6. Irimino-ana Cave	? <i>M. montebelli</i>	Shikama & Okafuji (1958)	Ditto.
7. Ohera-ana Cave	<i>M. montebelli</i>	Kawamura & Sotsuka (1984); this paper	
7. Ojika-do Cave	<i>M. montebelli</i>	Kawamura & Sotsuka (1984); this paper	

Holocene localities, however, the fossil *Microtus* is represented by a single species, *M. montebelli*. Such circumstances are identical with those of the present day.

Microtus is a highly adapted group for the life in grassland environments of the temperate zone. Since the Middle Pleistocene, it has been extensively spread over the Holarctic Region and differentiated into many species. In Japan, however, only a few species have been existent in any time of this period. One of them is predominant, but others are scarce or absent. Therefore it can be stated that the *Microtus* fauna in Japan has been poor in variety in comparison with other areas. It is related to the fact that the grassland dwellers have been very rare in the micro-mammalian faunas of Japan since the Middle Pleistocene. It is inferred that the sylvan environments have predominated during these periods, so that the preferable

habitats to *Microtus* have been restricted in Japan.

***Microtus montebelli* (MILNE-EDWARDS, 1872)**

(Figs. 137, 138, 140–143; Pls. 20–23)

Arvicola montebelli, MILNE-EDWARDS 1872, *Rech. Mamm.*, 285.

Synonym (living forms) —

Arvicola hatanezumii; SASAKI 1904, *Bull. Coll. Agr. Tokyo*, **6**, 51–55.

Microtus montebelli MILNE-EDWARDS; THOMAS 1905, *Proc. Zool. Soc. London*, **1905**, **2**, 352.

Microtus montebelli (MILNE-EDWARDS); AOKI 1915, *Nipponsan Nezumika (Japanese Muridae)*, 13–15.

Microtus montebelli (MILNE-EDWARDS); KISHIDA 1924, *Honyudobutsu Zukai (Monogr. Japanese Mamm.)*, 105–107.

Microtus montebelli (MILNE-EDWARDS); KINOSHITA 1928, *Res. Bull. Coll. Exp. Forests, Hokkaido Imp. Univ.*, **5**, 170–172.

Microtus montebelli MILNE-EDWARDS; WATANABE 1937, *Occ. Pap. Ibaraki Agr. St.*, (2), 8–17.

Microtus montebelli (MILNE-EDWARDS); HANAOKA 1937, *Zool. Mag.*, **49**, 273–274.

Microtus montebelli montebelli (MILNE-EDWARDS) and *M. m. brevicorpus* TOKUDA; KURODA 1940, *Monogr. Japanese Mamm.*, 101–102.

Microtus montebelli (MILNE-EDWARDS); TOKUDA 1941, *Trans. Biogeogr. Soc. Japan*, **4**, 58–61.

Microtus montebelli (MILNE-EDWARDS); IMAIZUMI 1949, *Nat. Hist. Japanese Mamm.*, 246–250.

Microtus montebelli MILNE-EDWARDS; ELLERMAN and MORRISON-SCOTT 1951, *Checklist of Palearctic and Indian Mammals*, 700.

Microtus montebelli (MILNE-EDWARDS); KURODA 1953, *Nippon Jurui Zusetsu (Monogr. Japanese Mamm.)*, 81.

Microtus montebelli MILNE-EDWARDS; IMAIZUMI 1960, *Coloured Illust. Mamm. Japan*, 139–140.

Microtus montebelli; CORBET 1978, *The Mammals of the Palearctic Region*, 115.

Synonym (fossil forms) —

Microtus montebelli montebelli; NAORA 1954, *Old Stone Age in Japan*, 227 (Fig. 162); from Izurugahara Cave (Kuzuü).

Microtus montebelli (MILNE-EDWARDS); TAKAI 1962, *Jour. Anthropol. Soc. Nippon*, **70**, 36, 38, 39; from Tadaki Quarry.

Microtus montebelli (MILNE-EDWARDS); KOWALSKI and HASEGAWA 1976, *Bull. Nat. Sci. Mus. Ser. C*, **2**, 54–57; from Shiriya Quarry, Takanosuzawa Cave (Kuzuü), Miyata First and Second Caves (=Okubo First and Second Caves respectively; Upper Kuzuü Formation), Aizawa (=Yoshizawa, Upper Kuzuü F.), Quarry no. 8 of Yoshizawa Sekkai Co. (Upper Kuzuü F.), Shiraiwa Mine, Ushikawa and Makurazino-ana Cave.

Microtus montebelli (MILNE-EDWARDS); KAWAMURA and ISHIDA 1976, *Jour. Speleol. Soc. Japan*, **1**, 33; from Kumaishi-do Cave.

Microtus montebelli (MILNE-EDWARDS); KAWAMURA 1977, *Fossil Club Bull.*, (14), 7; from Kumaishi-do Cave.

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

Microtus montebelli (MILNE-EDWARDS); KAWAMURA and TAMIYA 1980, *Bull. Akiyoshi-dai Mus. Nat. Hist.*, (15), 32; from Tanuki-ana Cave.

Microtus montebelli (MILNE-EDWARDS); KAWAMURA and KAJIURA 1980, *Jour. Speleol. Soc. Japan*, **5**, 53; from Sugi-ana Cave.

Microtus montebelli (MILNE-EDWARDS); 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.

Microtus montebelli (MILNE-EDWARDS); OKUMURA *et al.* 1982, *Earth Sci.*, **36**, 216; from Kumaishi-do Cave.

Microtus montebelli; KAWAMURA 1983, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, **6**, 58; from Anagami Rockshelter Site.

Microtus montebelli (MILNE-EDWARDS); KAWAMURA and SOTSUKA 1984, *Bull. Kitakyushu Mus. Nat. Hist.* (5), 171–172; from Seiryukutsu Cave and Ohera-ana Cave.

Microtus montebelli (MILNE-EDWARDS); 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****Locality 3 of Ube Kosan Quarry**

- Layer 1: 1 isolated M^3 (KUJC96006); 1 mandible with M_1 (KUJC96001).
 Layer 2: 2 isolated M^3 (KUJC96031, 96034).
 Layer 3: 2 isolated M^3 (KUJC96050, 96051).
 Layer 4: 3 isolated M^3 (KUJC96067–96069); 1 mandible with M_1 (KUJC97039); 5 isolated M_1 (KUJC97040–97044).
 Layer 5: 1 isolated M^3 (KUJC96176).
 Layer 6: 3 isolated M_1 (KUJC96259–96261).
 Layer 8: 6 isolated M^3 (KUJC96163–96168); 9 isolated M_1 (KUJC96146, 96147, 96149–96151, 96155, 97049, 97050, 97051).
 Layer 9: 4 isolated M^3 (KUJC96129, 96130, 96132, 96133); 2 isolated M_1 (KUJC97047, 97048).
 Layer 10: 2 isolated M^3 (KUJC96110, 96111); 5 isolated M_1 (KUJC96103–96105, 97045, 97046).
 Layer 11: 1 isolated M^3 (KUJC96251).
 Layer 12: 2 isolated M^3 (KUJC96243, 96244); 1 mandible with I , M_1 and M_2 (KUJC96230); 1 mandible with M_1 and M_2 (KUJC96232); 5 isolated M_1 (KUJC96231, 96233–96236).
 Layer 13: 12 isolated M^3 (KUJC96213–96224); 2 mandibles with I , M_1 and M_2 (KUJC96200, 96201); 2 mandibles with M_1 and M_2 (KUJC96202, 96208); 1 mandible with M_1 (KUJC96209); 6 isolated M_1 (KUJC96203–96207, 96210).
 Layer 14: 4 isolated M^3 (KUJC96194–96197); 1 mandible with M_1 and M_2 (KUJC96184); 7 isolated M_1 (KUJC96185–96191).
 Layer 17: 2 isolated M^3 (KUJC96095, 96097); 2 isolated M_1 (KUJC96089, 96090).
 Layer 18: 4 isolated M^3 (KUJC96074, 96083–96085); 1 mandible with M_1 and M_2 (KUJC96076); 4 isolated M_1 (KUJC96077–96080).
 Horizon unknown: 1 mandible with M_1 (KUJC96273).

Locality 1 of Ube Kosan Quarry

- 3 isolated M_1 from Layer 2 (ASM 701303–701305); 1 isolated M^3 from Layer 1 (ASM 701306).

LATE PLEISTOCENE LOCALITIES**Aisawa Quarry**

- 8 isolated M^3 (KUJC100042–100049); 5 isolated M_1 (KUJC100050–100054).

Sugi-ana Cave

- 57 isolated M^3 (KUJC100055–100111); 1 mandible with I and M_1 – M_3 (KUJC100112); 3 mandibles with I , M_1 and M_2 (KUJC100113, 100114, 100715); 2 mandibles with I and M_1 (KUJC100716, 100717); 49 isolated M_1 (KUJC100115–100163).

Yage Quarry (all except KUJC100164 are unnumbered specimens of the MATSUHASHI Collection)

- Site 1: 1 mandible with I , M_1 and M_2 ; 1 isolated M_1 .
 Site 2: 1 mandible with I , M_1 and M_2 .
 Site 4: 1 mandible with I , M_1 and M_2 ; 1 isolated M_1 (KUJC100164).
 Site 5: 1 mandible with I and M_1 – M_3 ; 2 mandibles with I , M_1 and M_2 ; 1 isolated M_1 .

Seiryukutsu Cave

- 1 isolated M_1 from Naumann Branch (KMNH VP 300,020)

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

- Horizon P: 17 isolated M^3 (K03018–03034); 26 isolated M_1 (K03035–03060).
 Horizon O (lower part): 13 isolated M^3 (K03061–03073); 1 mandible with I , M_1 and M_2 (K03074); 2 mandibles with M_1 and M_2 (K03075, 03076); 20 isolated M_1 (K03077–03088, 03787–03794).
 Horizon O (upper part): 60 isolated M^3 (K03089–03148); 1 mandible with I and M_1 – M_3 (K03149); 3 mandibles with I , M_1 and M_2 (K03150–03152); 1 mandible with I and M_1 (K04159); 1 mandible with M_1 (K03153); 73 isolated M_1 (K03154–03226).
 Horizon N: 28 isolated M^3 (K03227–03254); 63 isolated M_1 (K03255–03317).
 Horizon M (lower part): 4 isolated M^3 (K03318–03321); 1 mandible with M_1 (K03322); 16 isolated M_1 (K03323–03338).
 Horizon M (upper part): 151 isolated M^3 (K03339–03489); 2 mandibles with I , M_1 and M_2

(K03490, 03491); 1 mandible with M_1 and M_2 (K03492); 217 isolated M_1 (K03493–03709).

Kumaishi-do Cave

F_3 : 28 isolated M^3 (YKS 04076, 04079, 04080, 04083, 04084, 04087, 04092–04098, 04100, 04102, 04104, 04105, 04107, 04108, 04110–04117, 04348); 2 mandibles with M_1 (YKS 04013, 04022); 34 isolated M_1 (YKS 00022, 04031–04039, 04041–04043, 04045–04049, 04051, 04053, 04054, 04057–04065, 04069–04072).

F_1 , F_2 and F_4 : 42 isolated M^3 (YKS 00164, 00174, 00178–00182, 00184, 00186, 00188–00192, 00195, 00196, 00203, 00206, 00207, 00211, 00273, 00278a, 00278b, 00280, 00283, 03001–03012, 03014–03018); 1 mandible with I and M_1 (YKS 00288); 1 mandible with M_1 (YKS 00297); 32 isolated M_1 (YKS 00023, 00026–00028, 00032, 00034–00036, 00038, 00039, 00042–00044, 00048, 00049, 00057, 00058, 00063–00066, 00069, 00072, 00074, 00080, 00083, 00084, 00088, 00105, 00107–00109).

Site unknown

7 isolated M^3 (YKS 00166–00172); 1 mandible with I, M_1 and M_2 (YKS 00291); 9 isolated M_1 (YKS 00004–00009, 00012, 00013, 00040).

East Fissure of Suse Quarry (MATSUHASHI Collection, unnumbered)

1 fragmental skull with left M^1 – M^3 and right M^1 ; 1 maxillary fragment with M^1 , M^2 and M^3 ; 1 mandible with I and M_1 – M_3 .

HOLOCENE LOCALITIES

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

Horizon J: 1 mandible with M_1 , M_2 and M_3 (K04156); 2 mandibles with I, M_1 and M_2 (K03710, 03711); 1 mandible with M_1 and M_2 (K03712); 1 mandible with I and M_1 (K03713, 04157); 1 mandible with M_1 (K04158).

Horizon I: 1 fragmental skull with left I and M^3 , and right I, M^1 and M^3 (K03714); 1 isolated M^3 (K03715); 4 mandibles with I, M_1 and M_2 (K03716–03719); 4 mandibles with M_1 and M_2 (K03720–03723); 4 mandibles with I and M_1 (K03724–03726, 04155); 2 isolated M_1 (K03727, 03728).

Horizon unknown: 3 mandibles with I, M_1 and M_2 (K04149–04151); 3 mandibles with I and M_1 (K04152–04154).

Domen Cave Site (specimen numbers are prefixed by HUA)

7 isolated M^3 (D00070–00076); 1 mandible with M_1 (D00077); 4 isolated M_1 (D00078–00081).

Tanuki-ana Cave

Layer 4: 24 isolated M^3 (ASM 701307–701330); 18 isolated M_1 (ASM 701331–701348).

Layer 3: 5 isolated M^3 (ASM 701349–701353); 5 isolated M_1 (ASM 701354–701358).

Layers 3 to 2: 6 isolated M^3 (ASM 701359–701364); 2 mandibles with M_1 (ASM 701365, 701366); 1 isolated M_1 (ASM 701367).

Layer 2: 10 isolated M^3 (ASM 701368–701377); 1 mandible with M_1 and M_2 (ASM 701378); 1 mandible with M_1 (ASM 701379); 16 isolated M_1 (ASM 701380–701395).

Layer 1: 4 isolated M^3 (ASM 701396–701399).

Husen-ana Cave

1 isolated M_1 (ASM 701400).

Anagami Rock-shelter Site (Layer 4 in Grids A-1 and B-1)

1 mandible with M_1 and M_2 (HUA-A00009); 1 mandible with M_1 (HUA-A00010).

Kitoragawa Site

3 isolated M_1 (unnumbered).

Diagnosis

M^3 with complicate posterior loop which is mostly C- or F-shaped; LSA5 well-developed, so that LS_5/LS_4 is more than 0.45 and Wm/LS_4 is mostly less than 1.0. M_1 with five or six closed triangles; both BSA4 and BRA4 well-developed.

Description

Skull —

Only two skulls worthy to describe are obtained from the Holocene horizons of Kannondo Cave Site and East Fissure of Suse Quarry (Fig. 137). The interorbital region is somewhat constricted, but the temporal crests are indistinct. The incisive foramina are slender and terminate considerably anterior to the front margin of M^1 . The palatal structure at its posterior end is complicate as one of the generic characters already described.

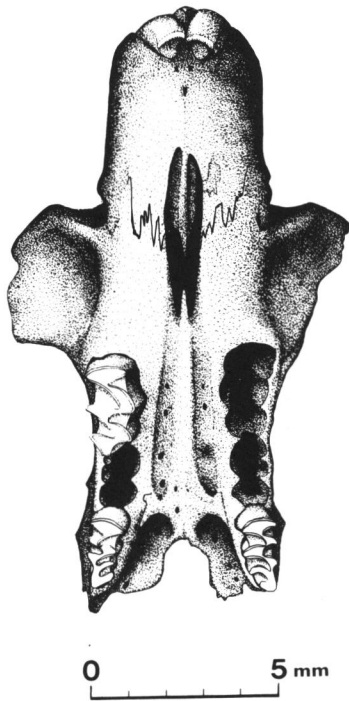


Fig. 137. Fragmental skull of *Microtus montebelli* from Horizon I (Holocene) of Kannondo Cave Site (HUA-K03714). Palatal view.

M^1 and M^2 —

The characters of these molars are identical with those described in p. 274 as the generic characters of the Japanese *Microtus*.

M^3 —

M^3 generally has four and three salient angles on the lingual and buccal sides respectively. The posterior loop is mostly C- or F-shaped. Specimens with E-shaped posterior loop are rarely found, in which five salient angles are present on the lingual side.

The posterior loop is generally narrow and slender. Because strong expansions or constrictions are not observed, its breadth is relatively constant. Exceptionally, a slight constriction at the bottom of LRA4 is rarely observed, which is resulted from the deep intrusion of LRA4 and usually from the slight development of BRA4. Wm/Ls_4 is mostly less than 1.0. The buccal face of the posterior loop is usually smooth without any projection, although a small additional

salient angle (BSA4) is sometimes observed at its anterior part. LSA4 strongly projects linguallly, and almost reaches at the level of LSA3. Well-developed LSA5 makes LRA4 a deep fold. LS_5/LS_4 is mostly more than 0.5. In the C-shaped posterior loop, LRA5 is absent, whereas it is recognized as a shallow fold in the F-shaped one. There exists a series of

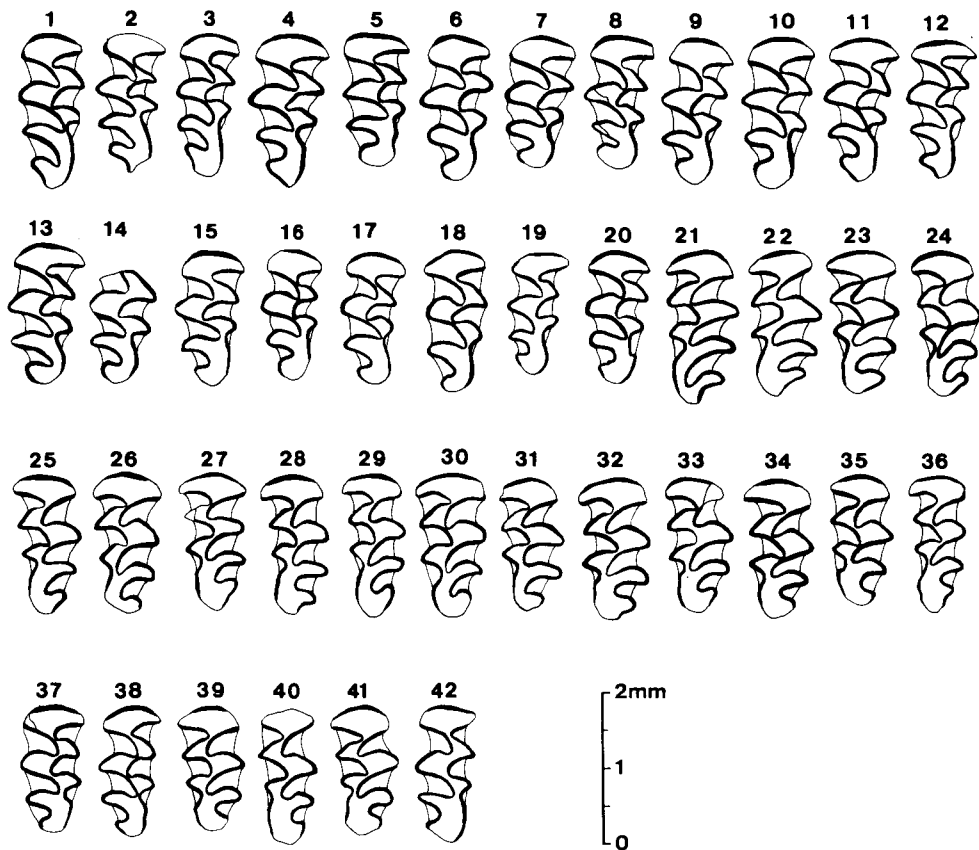


Fig. 138. Isolated M^3 of *Microtus montebelli* from Locality 3 of Ube Kosan Quarry. 1–20, 37, 38, 42, left M^3 ; 21–36, 39–41, right M^3 .

1, KUJC96244 from Layer 12; 2, KUJC96194 from Layer 14; 3, KUJC96216 from Layer 13; 4, KUJC96006 from Layer 1; 5, KUJC96031 from Layer 2; 6, 7, KUJC96050 and 96051 from Layer 3; 8, KUJC96110 from Layer 10; 9, KUJC96251 from Layer 11; 10, KUJC96243 from Layer 12; 11, 12, KUJC96214 and 96215 from Layer 13; 13, KUJC96163 from Layer 8; 14, KUJC96196 from Layer 14; 15, KUJC96095 from Layer 17; 16, KUJC96068 from Layer 4; 17, KUJC96111 from Layer 10; 18, 19, KUJC96164 and 96165 from Layer 8; 20, KUJC96213 from Layer 13; 21, KUJC96168 from Layer 8; 22, KUJC96218 from Layer 13; 23, KUJC96074 from Layer 18; 24, KUJC96132 from Layer 9; 25–29, KUJC96217, 96219, 96220, 96221 and 96223 respectively from Layer 13; 30, KUJC96097 from Layer 17; 31, KUJC96130 from Layer 9; 32, KUJC96224 from Layer 13; 33, KUJC96197 from Layer 14; 34, KUJC96069 from Layer 4; 35, KUJC96133 from Layer 9; 36, KUJC96222 from Layer 13; 37, KUJC96129 from Layer 9; 38, KUJC96195 from Layer 14; 39, KUJC96034 from Layer 2; 40–42, KUJC96084, 96085 and 96083 respectively from Layer 18.

intermediate forms in the development of this fold. In the extreme case (E-shaped one), LRA5 becomes a deep fold like LRA4. The length of the posterior loop (Lp) is relatively long, ranging 35–45% against the total length of M^3 . It is related to the shape of the posterior loop which is more advanced and complicate than those of *M. epiratticepoides* and *M. cf. brandtioides*. Exceptionally its length is somewhat shorter in the Middle Pleistocene population from Locality 3 of Ube Kosan Quarry than in the populations from other localities (Fig. 139).

Mandible —

The characters of the mandible are common to the generic characters of *Microtus* already described (Fig. 140). No significant differences are observed among the mandibles of the present fossils, *M. epiratticepoides* and *M. cf. brandtioides*. The mandibular foramen opens at the anterior face of the capsule for incisor on the lingual face of the ascending ramus. Its position corresponds to “*arvalis* type” by HALL and YALDEN (1978), but more anterior than that of *M. agrestis*.

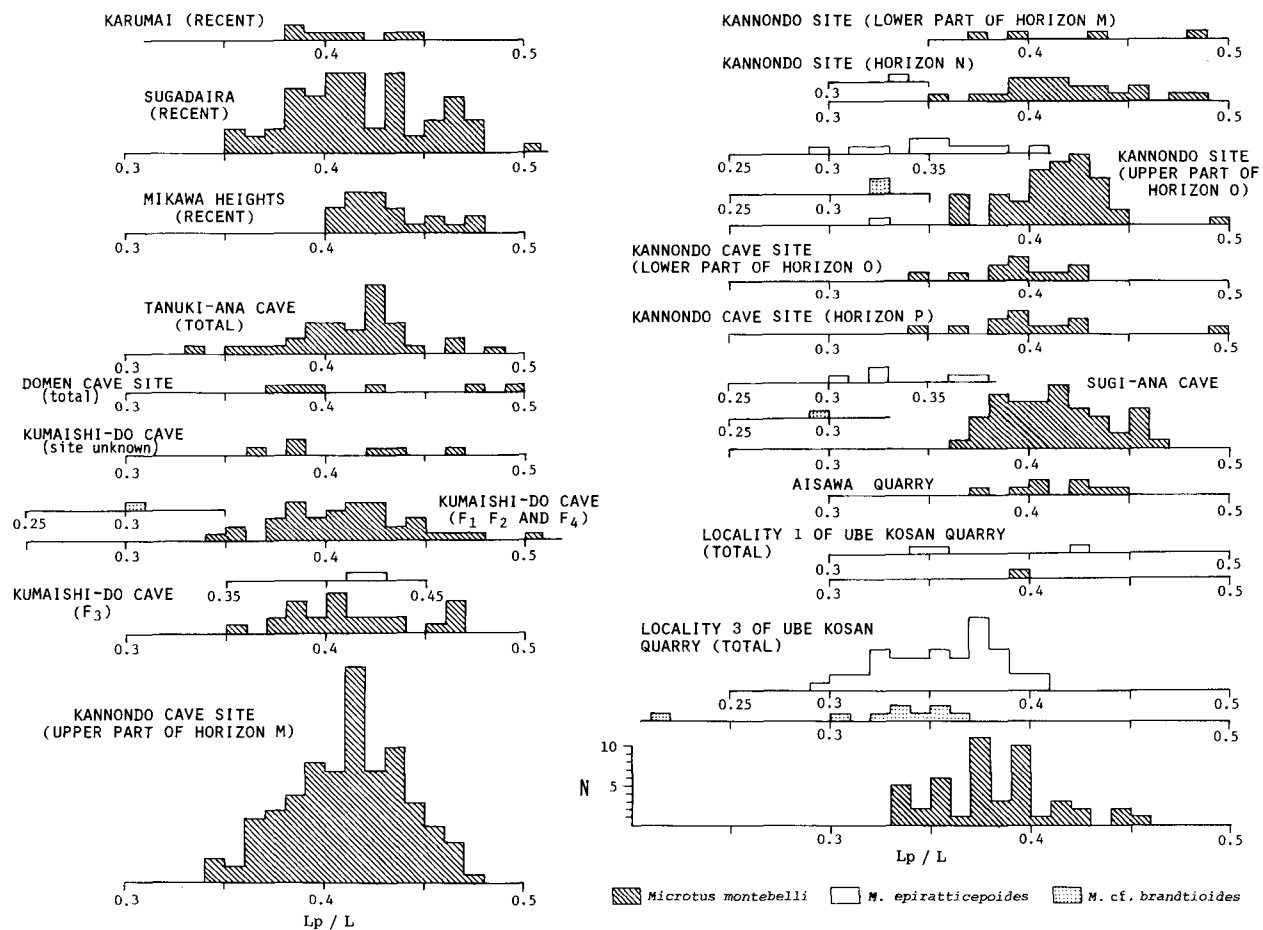
M_1 —

M_1 pattern is similar to that of *M. arvalis*. Is 1 to Is 6 are always closed, so that five closed triangles (T1–T5) are always formed between the anterior and posterior loops. The isthmus index is less than 2.0 (Fig. 126). Is 7 is mostly open, although it is sometimes closed by the deep intrusion of LRA4 toward the bottom of BRA4 to form the sixth closed triangle (T6; see Fig. 141). Five salient angles and five re-entrant angles are generally observed on the lingual side. On the other hand, four salient angles and four re-entrant angles are generally present on the buccal side. The most anterior salient angles (both LSA5 and BSA4) are well-developed as other salient angles. The relative position of LSA5 against BSA4 is variable in relation to the degree of the intrusion of LRA4. In some cases, LSA5 and BSA4 are opposite in position. In other cases, however, they are alternated in various degrees. The most anterior re-entrant angles (LRA5 and BRA4) are much shallower than others. The depths of these re-entrant angles are highly variable. When they are deeply intruded, the anterior loop is strongly constricted so that the additional salient angles (LSA6 and BSA5) are formed anterior to these re-entrant angles. In a few extreme cases, a faint re-entrant angle (LRA6) is observed on the anterior face of well-developed LSA6. When LRA5 and BRA4 are less developed, both LSA6 and BSA5 are not recognizable. The complexity of M_1 pattern depends mainly on the alternate position of LSA5 and BSA4, and the constriction between the bottoms of LRA4 and BRA4. The variation of these characters is described in the next section.

In younger individuals, each isthmus is rather broadly open than that of full-grown ones (Fig. 142). However the width of each isthmus is generally constant from Is 1 to Is 6. The pattern is fundamentally identical with that of the full-grown specimens. The cementum in each re-entrant angle is poorly developed and the enamel is thinner, although such characters are also found in younger specimens of other arvicolids.

M_2 and M_3 —

The characters of these molars are identical with those shared in the species of the Japanese *Microtus* (p. 274).

Fig. 139. Histograms of Lp/L in M³ of the Japanese *Microtus*.

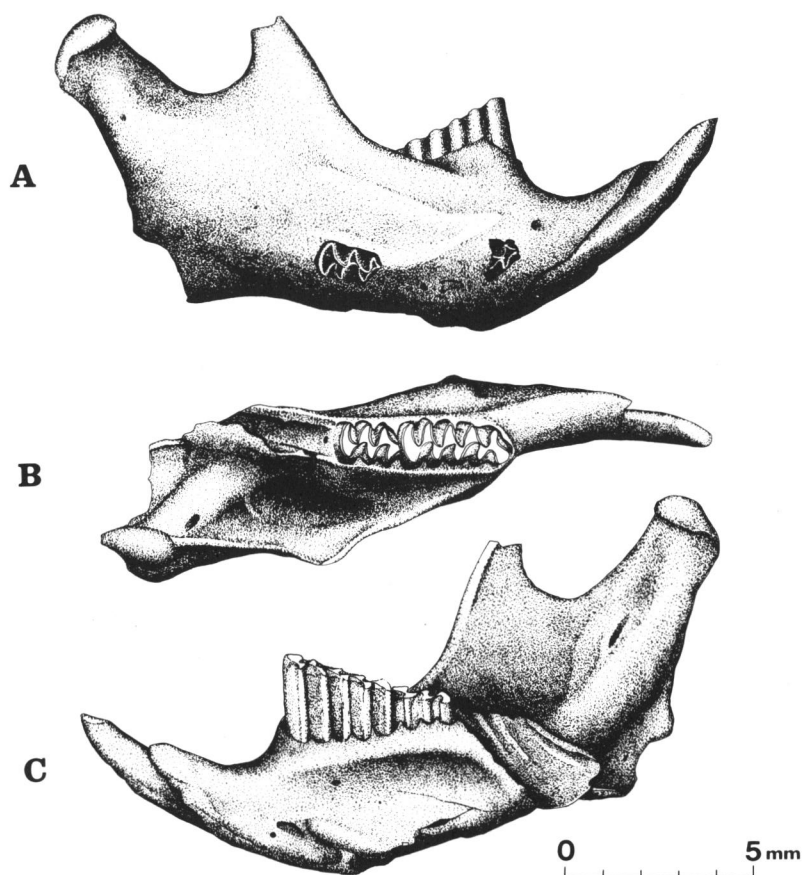


Fig. 140. Right mandible with I, M_1 and M_2 of *Microtus montebelli* from Horizon I of Kannondo Cave Site (HUA-K03718).

A, buccal view; B, upper view; C, lingual view.

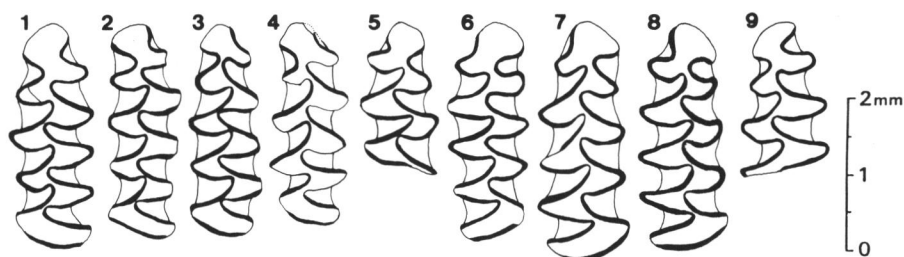


Fig. 141. *Microtus montebelli*. M_1 with six closed triangles (1-4, 9, left; 5-8, right). 1, KUJC100145 from Sugi-ana Cave; 2-5, specimens from the lower part of Horizon O of Kannondo Cave Site (2, HUA-K03082; 3, HUA-K03088; 4, HUA-K03792; 5, HUA-K03793); 6, HUA-K03163 from the upper part of Horizon O of Kannondo Cave Site; 7, 8, HUA-K03724 and 03728 respectively from Horizon I of Kannondo Cave Site; 9, ASM 701387 from Layer 2 of Tanuki-ana Cave.

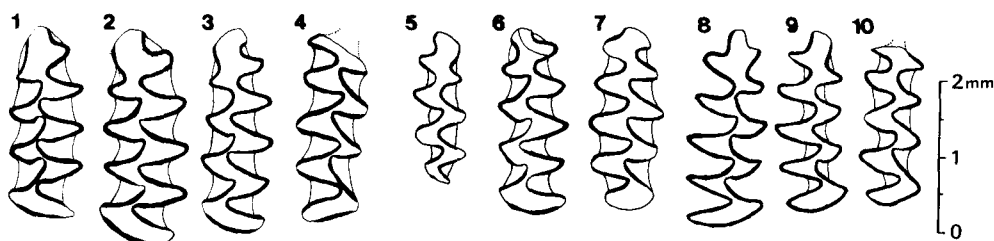


Fig. 142. *Microtus montebelli*. M_1 of young individuals (1–3, 6, left; 4, 5, 7–10, right). 1–4, specimens from Locality 3 of Ube Kosan Quarry (1, KUJJC96149 from Layer 8; 2, KUJJC96204 from Layer 13; 3, KUJJC96231 from Layer 12; 4, KUJJC96155 from Layer 8); 5–7, KUJJC100146 to 100148 respectively from Sugi-ana Cave; 8, YKS 00022 from F_3 of Kumaishi-do Cave; 9, HUA-K03725 from Horizon I of Kannondo Cave Site; 10, ASM 701388 from Layer 2 of Tanuki-ana Cave.

Morphological analysis of molars

M^3 —

The detailed morphology of the posterior loop is highly variable. In order to analyse its variation, all the fossil specimens are classified into the following morphotypes (Fig. 143). 106 recent specimens of *M. montebelli* are also examined for comparison.

- I. Normal type with Wm/Ls_4 less than 1.0, and Ls_5/Ls_4 more than 0.5. This type can be subdivided into the following five morphotypes:
 - Morphotype C₁*; posterior loop C-shaped, and BSA4 undeveloped.
 - Morphotype C₂*; posterior loop C-shaped, and BSA4 developed.
 - Morphotype F₁*; posterior loop F-shaped, and BSA4 undeveloped.
 - Morphotype F₂*; posterior loop F-shaped, and BSA4 developed.
 - Morphotype E*; posterior loop E-shaped with or without BSA4.
- II. Abnormal type with broad posterior loop (Wm/Ls_4 more than 1.0), but Ls_5/Ls_4 more than 0.5. The following subdivisions can be recognized:
 - Morphotype BC₁*; posterior loop C-shaped, and BSA4 undeveloped.
 - Morphotype BC₂*; posterior loop C-shaped, and BSA4 developed.
 - Morphotype BF₁*; posterior loop F-shaped, and BSA4 undeveloped.
 - Morphotype BF₂*; posterior loop F-shaped, and BSA4 developed.
- III. Abnormal type with reduced LSA5. Ls_5/Ls_4 less than 0.5. This type can be subdivided into the following two morphotypes:
 - Morphotype R₁*; posterior loop simple C-shaped, Ls_5/Ls_4 ranging from 0.45 to 0.5 (rarely 0.4 to 0.45), and Wm/Ls_4 less than 1.0.
 - Morphotype R₂*; posterior loop very simple C-shaped or upside-down L-shaped. Consequently this morphotype is indistinguishable from M^3 of *M. epiratticepoides*.

The number of the specimens belonging to each morphotype is shown in Table 64. The percentages in the main fossil localities (where more than 40 specimens are obtained) and in the recent population are given in Fig. 144.

The normal type (the morphotypes C_1 , C_2 , F_1 , F_2 and E) is most abundantly found in both fossil and recent populations. Its frequency attains to 74–96% in the fossil populations, and is higher in the Late Pleistocene and Holocene localities (85–96%) than in the Middle Pleistocene locality (74% in Locality 3 of Ube Kosan Quarry). In the recent population, this type is

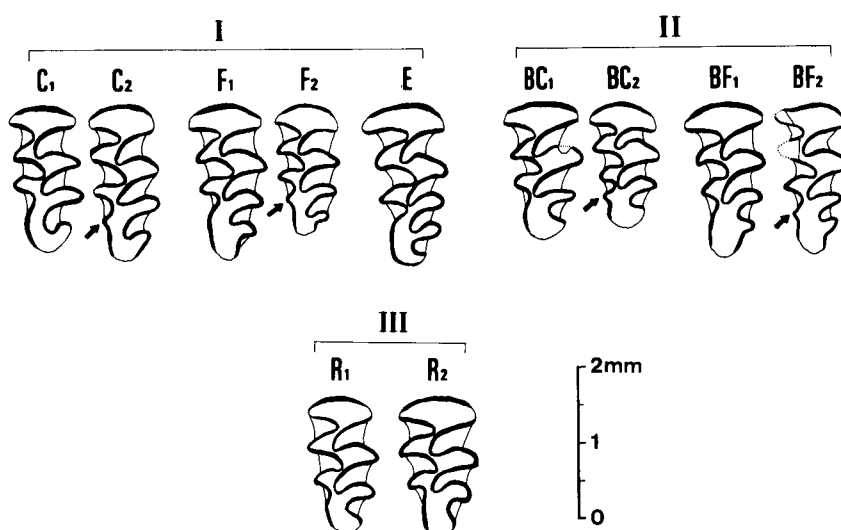


Fig. 143. Morphotypes of M^3 in *Microtus montebelli*. I, normal type comprising the morphotypes C_1 , C_2 , F_1 , F_2 and E ; II, abnormal type with broad posterior loop comprising the morphotypes BC_1 , BC_2 , BF_1 and BF_2 ; III, abnormal type with reduced LSA5 comprising the morphotypes R_1 and R_2 . The detailed explanation is given in the text. Arrow indicates BSA4. The following specimens are illustrated as examples:

C_1 , left M^3 from Domen Cave Site (HUA-D00070); C_2 , left M^3 from Layer 2 of Tanuki-ana Cave (ASM 701368); F_1 , F_2 , left M^3 from the lower part of Horizon O of Kannondo Cave Site (HUA-K03061, 03062); E , left M^3 from Domen Cave Site (HUA-D00072); BC_1 , left M^3 from the upper part of Horizon M of Kannondo Cave Site (HUA-K03339); BC_2 , right M^3 from Sugi-ana Cave (KUJC100055; this figure is turned over for comparison with other specimens); BF_1 , right M^3 of a recent specimen from Mikawa Heights (this figure is also turned over); BF_2 , left M^3 from the upper part of Horizon M of Kannondo Cave Site (HUA-K03340); R_1 , left M^3 from Layer 5 of Locality 3 of Ube Kosan Quarry (KUJC96176); R_2 , left M^3 of a recent specimen from Sugadaira (KANAMORI Collection).

observable in 92% of the total specimens, which approximates the frequencies in the Late Pleistocene and Holocene localities.

Among the subdivisions of the normal type, the morphotypes C_1 and F_1 are most abundant, whereas C_2 and F_2 are rather few. Moreover the morphotype E is much fewer. Although the frequencies of the morphotypes C_1 and F_1 considerably fluctuate from locality to locality, C_1 is more frequently found than F_1 in both fossil and recent populations except in Sugi-ana Cave. Because the morphotypes C_2 and F_2 are characterized by the development of BSA4, the relative scarcity of these morphotypes indicates that the appearance of BSA4 is rather few in the examined populations.

The abnormal type with broad posterior loop (morphotypes BC_1 , BC_2 , BF_1 and BF_2) uncommonly occurs in both fossil and recent populations (2–14% and 3% respectively). The frequency in the Middle Pleistocene locality (Locality 3 of Ube Kosan Quarry) is somewhat higher than those of the Late Pleistocene, Holocene and recent populations. The occurrences

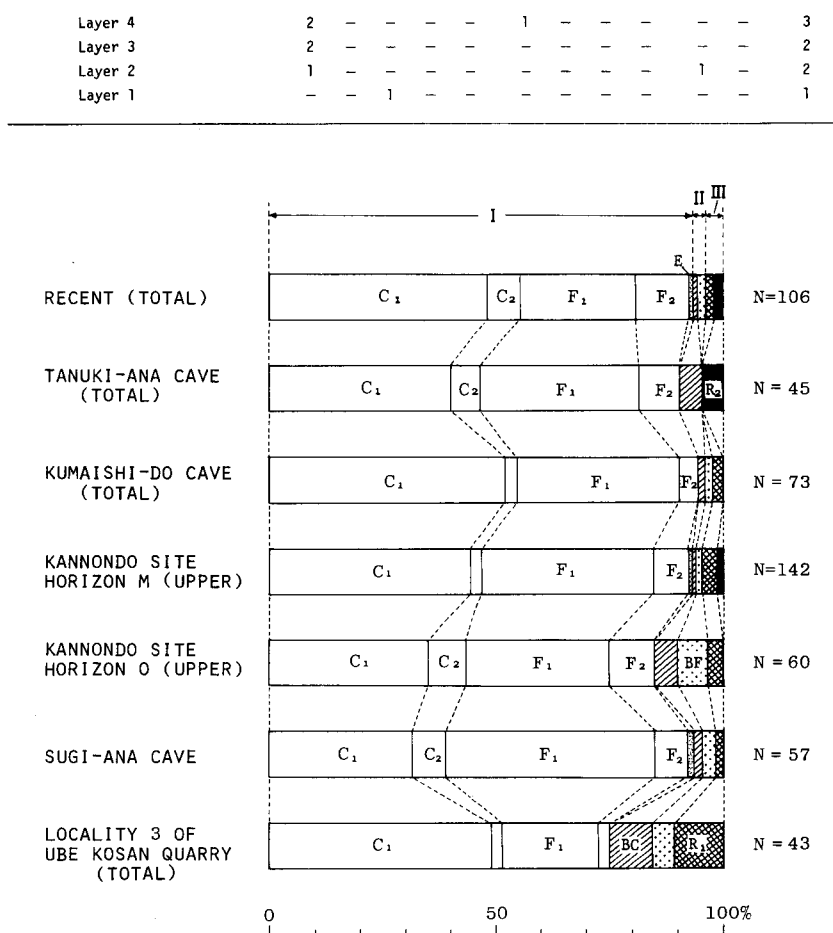


Fig. 144. Frequency of each morphotype in M^3 of *Microtus montebelli*. The percentages are given. N, total number of the examined specimens in each population.

of each subdivided variant (BC_1 , BC_2 , BF_1 and BF_2) are further rare.

The abnormal type with reduced LSA5 (the morphotypes R_1 and R_2) are also rarely found in both fossil and recent populations (1–12% and 4% respectively). The present analysis of the recent materials reveals that the reduced LSA5 is sometimes observed in younger individuals of *M. montebelli*, but becomes very rare in full-grown ones. Although young individuals are eliminated from the analysed fossil populations, some adolescent ones are probably included in the populations. The presence of the specimens with the R_1 and R_2 patterns in the fossil populations is partly attributable to such age variation. However some recent adult specimens exactly have the R_1 or even R_2 patterns.

The occurrence of the morphotype R_2 in the recent population suggests that there are a few specimens of *M. montebelli* with the pattern indistinguishable from that of *M. epiratticepoides*,

although their frequency is very low (less than 2%)*. Therefore, in the present study, any specimens are not classified into R_2 of *M. montebelli* in the fossil populations where the coexistence of *M. montebelli* and *M. epiratticepoides* is confirmed by M_1 (Table 64, Fig. 144). On the other hand, R_2 is recognized in the populations where M_1 of *M. montebelli* are exclusively obtained (for example, Tanuki-ana Cave)*.

The morphotype R_1 of *M. montebelli* can be regarded as a transitional form to the M^3 pattern of *M. epiratticepoides*. This morphotype is however distinguishable from M^3 of *M. epiratticepoides* by more developed LSA5 and slenderer posterior loop. This morphotype is rare in the Late Pleistocene and Holocene localities (0–3%) as well as in the recent population (2%). However its frequency increases in the Middle Pleistocene locality (12%).

M_1 —

The morphological variation of the anterior loop is considerably high in the present fossils. The morphotype analysis is carried out in all the fossil specimens and the recent comparative materials (105 individuals). The following six morphotypes are recognized in accordance with the relative position of LSA5 and BSA4, the degree of the development of these salient angles and the formation of the closed T6 (Fig. 145):

Morphotype O: Opposite type; namely LSA5 is situated in the opposite position against BSA4. The line from the lateral tip of LSA5 to that of BSA4 (a–b in Fig. 145) runs through the interior of the anterior loop. The length between the deepest points of LRA4 and BRA3 (l in Fig. 145) is less than 0.1 mm.

Morphotype I_1 : Intermediate type between the morphotypes O and A, but somewhat near to O. The line (a–b) runs through the interior of the anterior loop, whereas the length (l) is more than 0.1 mm.

Morphotype I_2 : Intermediate type between the morphotypes O and A, but somewhat near to A. The line (a–b) passes on the enamel layer at the bottom of LRA4.

Morphotype A: Alternate type; namely LSA5 is situated in the alternate position against BSA4. The line (a–b) runs through the interior of LRA4. The length (l) is much longer than those of the morphotypes I_1 and I_2 .

Morphotype Act: Morphotype with an additional closed triangle (T6). LSA5 is situated in the alternate position against BSA4. Is 7 is closed by the deep intrusion of LRA4 toward BRA4. Consequently six closed triangles are formed between the shortened anterior loop and posterior loop.

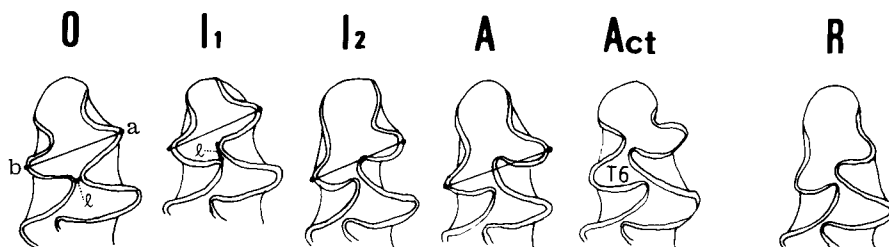


Fig. 145. Morphotypes of M_1 of *Microtus montebelli*. The anterior part of the crown is shown. a–b, line from the lateral tip of LSA5 (a) to that of BSA4 (b); l , length between the deepest points of LRA4 and BRA3 (both points are defined at the inner faces of the enamel bands). For detailed explanation see text.

* See Fig. 130. The individuals with the R_2 pattern are indicated by arrows.

Table 65. Frequency of each morphotype in M_1 of *Microtus montebelli*. The number of the specimens belonging to each morphotype is given.
 * KANAMORI Collection; ** MATSUHASHI Collection (mostly);
 ○ Grids A-I and B-1. For explanation of each morphotype see Fig. 145 and text.

LOCALITY	M O R P H O T Y P E S O F M_1						TOTAL
	0	I_1	I_2	A	Act	R	
RECENT MATERIALS							
Karumai	5	—	—	1	—	—	6
Sugadaira*	29	37	6	2	2	—	76
Mikawa Heights	6	4	7	1	5	—	23
HOLOCENE							
Kitoragawa Site	—	1	1	1	—	—	3
Anagami Site (Layer 4)*	1	1	—	—	—	—	2
Husen-ana Cave	1	—	—	—	—	—	1
Tanuki-ana Cave							
Layer 2	9	3	3	1	1	1	18
Layers 2 to 3	1	1	1	—	—	—	3
Layer 3	3	2	—	—	—	—	5
Layer 4	5	7	6	—	—	—	18
Domen Cave Site							
Horizon unknown	—	1	—	—	—	—	1
Horizon V (upper)	2	—	—	—	2	—	4
Kannondo Cave Site							
Horizon I	4	1	4	1	3	—	13
Horizon J	2	1	1	—	—	—	4
LATE PLEISTOCENE							
Suse Quarry (East Fissure)**	1	—	—	—	—	—	1
Kumaishi-do Cave							
Site unknown	4	3	3	—	—	—	10
F_1 , F_2 and F_3	21	11	1	—	—	—	33
F_3	12	17	5	—	2	—	36
Kannondo Cave Site							
Horizon M (upper)	71	86	31	6	14	—	208
Horizon M (lower)	7	6	—	1	1	—	15
Horizon N	23	20	10	1	4	—	58
Horizon O (upper)	22	31	12	5	5	2	77
Horizon O (lower)	5	6	2	—	2	—	15
Horizon P	8	8	3	7	—	—	26
Seiryukutsu Cave	—	—	1	—	—	—	1
Yage Quarry**							
Site 1	1	—	1	—	—	—	2
Site 2	1	—	—	—	—	—	1
Site 4	1	—	1	—	—	—	2
Site 5	2	—	2	—	—	—	4
Sugi-ana Cave	31	12	6	1	1	—	51
Aisawa Quarry	5	—	—	—	—	—	5
MIDDLE PLEISTOCENE							
Loc. 1 of Ube Kusan Quarry							
Layer 2	—	1	—	1	—	1	3
Loc. 3 of Ube Kusan Quarry							
Horizon unknown	—	1	—	—	—	—	1
Layer 18	2	3	—	—	—	—	5
Layer 17	1	1	—	—	—	—	2
Layer 14	7	—	2	—	—	—	9
Layer 13	4	3	2	2	—	—	11
Layer 12	3	1	2	—	—	1	7
Layer 10	3	2	—	—	—	—	5
Layer 9	1	1	—	—	—	—	2
Layer 8	3	1	3	1	—	—	8
Layer 6	2	—	1	—	—	—	3
Layer 4	2	1	2	1	—	—	6
Layer 1	1	—	—	—	—	—	1

These five morphotypes are normal as the M_1 pattern of *M. montebelli*. They are characterized by the well-developed LSA5 and BSA4, and by the well-defined LRA5 and BRA4. In the following morphotype, these salient and re-entrant angles are somewhat reduced:

Morphotype R: Reduced type; namely LSA5 and BSA4 are somewhat poorly developed. Consequently LRA5 and/or BRA4 become shallow (39 and 40 of Pl. 23).

The number of the specimens belonging to each morphotype is given in Table 65. The percentages in the main fossil localities (where more than 40 specimens are obtained) and in the recent population are also illustrated in Fig. 146.

The morphotypes O and I_1 are most abundant in the fossil and recent populations. Their percentages fluctuate between 69% and 91%. The frequency of the morphotype O approximates to that of I_1 in the recent population, whereas it exceeds I_1 in the fossil populations except two horizons (M and O) of Kannondo Cave Site. The morphotype I_2 occurs less abundantly than I_1 in both fossil and recent populations (11–23% and 12% respectively). The frequency of the morphotype A (2–7%) is much lower than that of I_2 . The morphotype

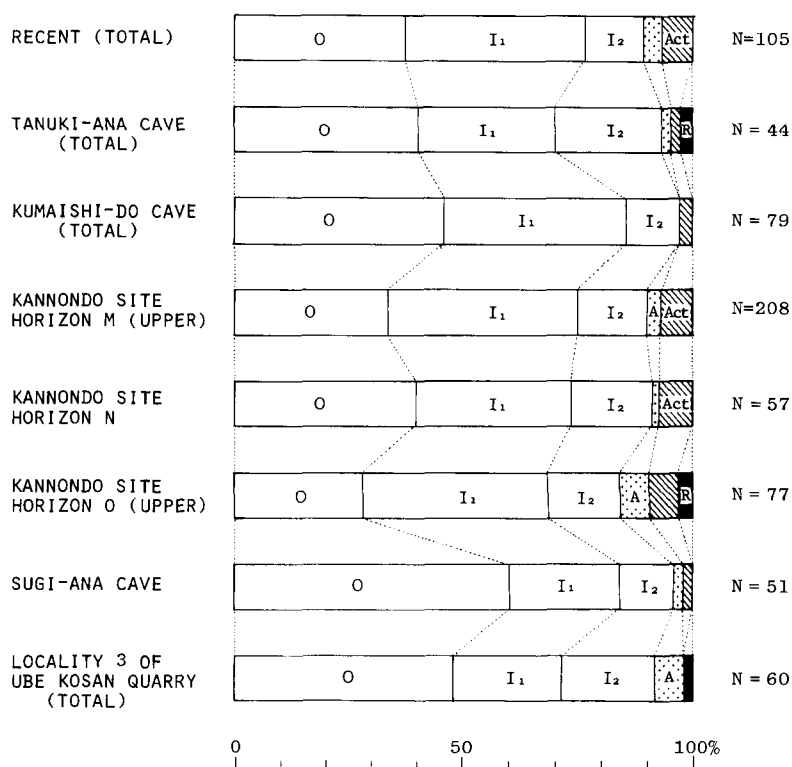


Fig. 146. Frequency of each morphotype in M_1 of *Microtus montebelli*. The percentages are given. N, total number of the examined specimens in each population.

Act is equal in number to or somewhat more than A, but its frequency is generally low (2–7%). This morphotype does not appear in the Middle Pleistocene locality. The morphotype R is found only in four localities (Table 65). Its frequency is much lower (0–3%).

Measurements

The measurements of the mandibles and molars are given in Tables 66–70.

Comparisons

The fossil specimens described here are well coincident with the living *Microtus montebelli* in the osteological and dental characters. Therefore they are undoubtedly referred to *M. montebelli*. This conclusion is supported by the comparisons given below, although the close relationship with *M. maximowiczii* and *M. arvalis* is also suggested.

Numerous species of the genus *Microtus* (*sensu lato*) are known from the Holarctic Region. Among them, the species of the subgenera *Allophaomys*, *Phaiomys* (*sensu* CHALINE, 1974b) and *Pedomys* are readily distinguishable from the present fossils by the presence of only three closed triangles in M_1 and by M^3 with simpler pattern. On the other hand, the typical species of the subgenus *Pitymys* (sometimes considered as a full genus) are characterized by the broad confluence of T4 with T5 in M_1 , whereas they are always completely separated in the present fossils.

Comparisons with the living species of Microtus known from East Asia —

As the species of *Microtus* other than those of the above-mentioned subgenera, the following are known only from East Asia in accordance with CORBET (1978):

- Microtus sikimensis* (HODGSON, 1849)
- Microtus bedfordi* (THOMAS, 1911)
- Microtus brandtii* (RADDE, 1861)
- Microtus mandarinus* (MILNE-EDWARDS, 1871)
- Microtus fortis* BÜCHNER, 1889
- Microtus clarkei* HINTON, 1923
- Microtus millicens* THOMAS, 1911
- Microtus kikuchii* KURODA, 1920
- Microtus mongolicus* (RADDE, 1862)
- Microtus sachalinensis* VASIN, 1955
- Microtus maximowiczii* (SCHRENK, 1859)

Microtus sikimensis which was allocated to the genus *Pitymys* by CORBET (1978) is distributed in Himalaya and South China (Szechuan and South Kansu). Although *M. forresti* (HINTON) and *M. irene* THOMAS are included in *M. sikimensis* by CORBET, the molar patterns of these three forms are considerably different from each other. In the illustration of HINTON (1926, Fig. 29), “*sikimensis*” has a postero-lingual extra angle both in M^1 and in M^2 like *M. agrestis*. This character is never observed in the present fossils. M^3 of “*sikimensis*” is somewhat similar to that of the present fossils in having C-shaped posterior loop. The morphological similarity between them is also found in the anterior loop of M_1 , but M_1 of “*sikimensis*” carries

Table 66. Measurements of the mandibles of *Microtus montebelli* in mm. The numbers on the left side correspond to those in Fig. 72.

	Anaga- mi Site	Kannondo Cave Site (Holocene horizons)									
		Horizon unknown					Horizon I				
		HUA-A 00009	HUA-K 04149	HUA-K 04152	HUA-K 04153	HUA-K 04150	HUA-K 04154	HUA-K 04151	HUA-K 03716	HUA-K 03720	HUA-K 03721
2. Total length of the mandible (id to the condyle)	—	—	16.83±	—	—	—	—	—	—	—	—
3. Length from the tip of the incisor to the condyle	—	—	18.11	—	—	—	—	—	—	—	—
4. Length of the horizontal ramus	—	—	—	—	—	—	—	—	—	—	—
5. Length of the diastema	—	4.15±	4.26±	—	—	—	—	4.00	—	4.46±	—
6. Length of the ascending ramus (the posterior border of M ₃ to the condyle)	—	—	—	—	—	—	—	—	—	—	—
7. Ditto (the posterior border of M ₃ to gon)	—	—	—	—	—	—	—	—	—	—	—
12. Maximum height of the horizontal ramus	—	3.74	3.91	3.99	3.71	—	3.67	3.61	3.54	4.03	—
13. Height of the horizontal ramus behind M ₃	—	—	—	—	—	—	—	—	—	—	—
14. Maximum thickness of the horizontal ramus	—	2.72	3.30	3.04	3.31	2.93	2.79	2.78	2.90	3.01	—
15. Length of the molar row (M ₁ to M ₃) at the crowns	—	—	—	—	—	—	—	—	—	—	—
16. Ditto at the alveoli	—	—	—	6.39	6.57	—	—	—	—	—	—
17. Length of the molar row (M ₁ to M ₃) at the crowns	4.90	4.45	—	—	4.68	—	4.42	4.24	4.44	4.53	—
18. Ditto at the alveoli	5.13	4.61	4.91	4.68	4.71	4.67±	4.54±	4.33	4.50	4.64	—

Kannondo Cave Site (Holocene horizons)																
Horizon I										Horizon J						
HUA-K 03722	HUA-K 03717	HUA-K 03724	HUA-K 03718	HUA-K 03723	HUA-K 03725	HUA-K 03719	HUA-K 03726	HUA-K 04155	HUA-K 03710	HUA-K 03712	HUA-K 03713	HUA-K 03711	HUA-K 04156	HUA-K 04157	HUA-K 04158	
2.	—	—	17.06±	16.13±	—	13.45	—	—	—	—	16.63±	—	—	—	—	
3.	—	—	18.75	17.57	—	—	—	—	—	—	18.59±	—	—	—	—	
4.	—	—	—	9.88	—	—	—	—	—	—	10.89±	—	—	—	—	
5.	—	3.83±	4.40±	3.59±	—	3.90	—	4.50±	4.00±	4.44±	—	3.97±	4.11±	—	4.44±	4.78±
6.	—	—	—	7.03	—	—	—	—	—	—	7.36±	—	—	—	—	
7.	5.90±	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
12.	3.98	3.55	4.08	3.49	3.88	3.35	3.42	—	3.25	3.92	3.85	3.78	3.55	—	3.62	—
13.	—	—	—	—	—	—	—	—	—	—	—	—	—	2.13	—	—
14.	3.27	3.01	3.03	3.24	3.25	2.70	3.10	—	2.69	3.52	3.22	2.98	—	—	2.92	—
15.	—	—	—	—	—	—	—	—	—	—	—	—	—	5.15	—	—
16.	7.01±	6.28±	—	6.44	—	—	6.50	—	—	—	—	6.95	—	5.48	—	—
17.	5.08	4.49	—	4.58	4.99	—	4.33	—	—	4.72	4.67	—	4.27	3.89	—	—
18.	5.02	4.61	4.77	4.75±	5.24	4.14	4.70	—	4.38±	4.80	5.07	4.92	4.43	4.06	4.53±	—

Table 66. (Continued)

	Kumaishi-do Cave					Kannondo Cave Site (Late Pleistocene horizons)										Sugi-ana Cave	
	F ₄		F ₂		F ₃	Horizon 0 (upper part)						Horizon 0 (lower)					
	YKS	YKS	YKS	YKS	YKS	HUA-K	HUA-K	HUA-K	HUA-K	HUA-K	HUA-K	HUA-K	HUA-K	HUA-K	KUJC	KUJC	
	00288	00291	00297	04013	04022	03153	04159	03150	03151	03152	03149	03076	03075	03074	100113	100112	
2.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
3.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
4.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
5.	3.92	3.75	3.80±	—	—	4.09±	4.44	3.92±	—	—	—	—	—	—	4.64	—	
6.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
7.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
12.	2.95±	3.24	—	3.26	—	3.74	3.80	3.26	3.76	—	3.73	—	—	3.68	3.66	3.68±	
13.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
14.	2.89	2.62	—	2.78	2.76	2.97	3.06	2.79	2.99	3.00	3.07	—	—	3.18	—	2.96	
15.	—	—	—	—	—	—	—	—	—	6.03	—	—	—	—	—	5.83±	
16.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6.46±	6.36±	
17.	—	4.23	—	—	—	—	—	4.36	4.59	4.44	4.63	4.75	4.72±	4.72	4.33	4.12±	
18.	—	4.48	—	4.38	4.38	4.86	5.13	4.35	4.72	4.45	4.66	—	4.73±	4.82	4.62	4.49±	

	Sugi-ana Cave				Locality 3 of Ube Kosan Quarry											
					Horizon unknown		Layer 18		Layer 13					Layer 12		Layer 4
					KWJC 96273	KWJC 96076	KWJC 96200	KWJC 96201	KWJC 96202	KWJC 96208	KWJC 96209	KWJC 96230	KWJC 96232	KWJC 97039		
	KWJC 100715	KWJC 100114	KWJC 100716	KWJC 100717												
2.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
3.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
4.	—	—	—	—	—	—	—	—	—	—	—	—	10.30±	—	—	
5.	4.58	4.13	3.58±	—	3.73±	3.97	3.53±	3.60±	—	—	4.01±	—	3.97±	3.29±	—	
6.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
7.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
12.	3.67	3.22	3.13	3.42±	—	—	3.48	3.37	—	—	—	—	3.32	3.47	—	
13.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
14.	3.00	2.72	2.53	3.11	—	2.87	2.83	2.65	—	3.51	2.94	3.06	2.99	2.82	—	
15.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
16.	—	—	—	—	—	—	—	—	—	—	—	6.57±	6.34±	—	—	
17.	4.16±	4.39	—	—	—	4.00	4.38	3.95	4.22	4.24	—	4.60	4.45	—	—	
18.	4.68±	4.59	—	—	—	4.24	4.49	4.06	4.39±	4.32	—	4.64±	4.65	4.54	—	

Table 67. Measurements of M^3 of *Microtus montebelli* in mm. * KANAMORI Collection;
 ** MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
Karumai	6	1.77	1.95	2.19	0.15	6	0.88	0.96	1.04	0.07
Sugadaira*	74	1.48	1.92	2.39	0.19	74	0.62	0.95	1.14	0.12
Kurehayama	1	—	1.79	—	—	1	—	0.93	—	—
Mikawa Heights	23	1.36	2.11	2.40	0.20	23	0.71	1.01	1.11	0.08
HOLOCENE										
Tanuki-ana Cave										
Layer 1	4	1.93	1.99	2.04	—	3	0.87	0.93	1.03	—
Layer 2	6	1.92	2.11	2.32	0.16	7	0.76	0.95	1.04	0.05
Layers 2 to 3	5	1.83	1.98	2.12	0.10	5	0.88	0.95	1.00	0.04
Layer 3	4	1.58	1.87	2.13	—	4	0.86	0.94	1.00	—
Layer 4	16	1.56	1.95	2.44	0.25	17	0.70	0.90	0.99	0.09
Domen Cave Site										
Horizon unknown	1	—	2.02	—	—	2	0.95	1.00	1.05	—
Horizon V (upper)	4	1.83	2.08	2.29	—	5	0.98	1.00	1.04	0.03
Horizon V (lower)	2	1.87	1.92	1.98	—	2	0.94	0.99	1.03	—
Kannonodo Cave Site										
Horizon I	3	1.91	1.97	2.07	—	3	0.95	0.98	1.04	—
LATE PLEISTOCENE										
Suse Quarry (East Fissure)**	2	2.10	2.11	2.13	—	2	1.02	1.03	1.03	—
Kumaishi-do Cave										
Site unknown	5	1.80	1.95	2.16	0.15	7	0.90	0.94	0.98	0.03
F ₁ , F ₂ and F ₄	35	1.62	1.86	2.09	0.11	40	0.74	0.91	1.02	0.06
F ₃	26	1.56	1.84	2.10	0.11	28	0.72	0.88	0.99	0.07
Kannonodo Cave Site										
Horizon M (upper)	138	1.56	1.98	2.36	0.16	142	0.68	0.98	1.13	0.08
Horizon M (lower)	4	1.95	2.11	2.28	—	4	0.97	1.03	1.08	—
Horizon N	20	1.66	1.96	2.24	0.16	25	0.77	0.92	1.04	0.07
Horizon O (upper)	46	1.56	1.95	2.18	0.14	48	0.76	0.93	1.08	0.08
Horizon O (lower)	8	1.68	1.89	2.06	0.14	8	0.73	0.90	1.02	0.09
Horizon P	12	1.67	1.95	2.45	0.18	14	0.79	0.93	1.02	0.07
Sugi-ana Cave	49	1.57	1.88	2.17	0.15	52	0.76	0.90	1.01	0.07
Aisawa Quarry	8	1.85	2.10	2.31	0.13	8	0.95	1.02	1.11	0.06
MIDDLE PLEISTOCENE										
Locality 1 of Ube Kosan Quarry (Layer 1)	1	—	2.09	—	—	1	—	0.95	—	—
Loc. 3 of Ube Kosan Quarry										
Layer 18	4	1.71	1.80	1.91	—	4	0.79	0.85	0.96	—
Layer 17	2	1.78	1.85	1.93	—	2	0.85	0.91	0.96	—
Layer 14	3	1.70	1.75	1.79	—	3	0.77	0.83	0.88	—
Layer 13	12	1.72	1.84	1.91	0.05	12	0.79	0.88	0.99	0.05
Layer 12	2	1.99	2.00	2.01	—	2	0.91	0.92	0.94	—
Layer 11	1	—	1.92	—	—	1	—	0.90	—	—
Layer 10	2	1.74	1.75	1.77	—	2	0.85	0.86	0.86	—
Layer 9	4	1.68	1.78	1.91	—	4	0.79	0.87	0.90	—
Layer 8	5	1.64	1.86	2.04	0.13	5	0.76	0.94	1.10	0.12
Layer 5	1	—	1.81	—	—	1	—	0.95	—	—
Layer 4	3	1.72	1.87	2.04	—	3	0.80	0.90	0.97	—
Layer 3	2	1.78	1.85	1.92	—	2	0.89	0.92	0.95	—
Layer 2	2	1.65	1.70	1.75	—	2	0.88	0.88	0.88	—
Layer 1	1	—	2.05	—	—	1	—	1.03	—	—

Table 68. Measurements of M_1 of *Microtus montebelli* in mm. * KANAMORI Collection; ** MATSUHASHI Collection (mostly); ○ Grids A-1 and B-1. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
Karumai	6	2.62	2.89	3.13	0.17	6	1.06	1.14	1.21	0.06
Sugadaira*	74	2.51	2.90	3.63	0.20	74	0.98	1.17	1.36	0.09
Mikawa Heights	23	2.64	3.07	3.32	0.15	23	0.97	1.23	1.35	0.08
HOLOCENE										
Kitoragawa Site	3	2.91	2.97	3.07	—	3	1.18	1.21	1.27	—
Anagami Site (Layer 4)°	1	—	3.27	—	—	2	1.18	1.18	1.19	—
Husen-ana Cave	—	—	—	—	—	1	—	1.15	—	—
Tanuki-ana Cave										
Layer 2	8	2.57	2.86	3.13	0.19	12	0.91	1.04	1.17	0.07
Layers 2 to 3	2	2.96	2.98	2.99	—	2	1.08	1.09	1.10	—
Layer 3	4	2.69	2.85	3.01	—	4	0.92	1.06	1.16	—
Layer 4	5	2.75	2.94	3.09	0.12	7	1.06	1.15	1.24	0.06
Domen Cave Site										
Horizon unknown	1	—	2.79	—	—	1	—	1.14	—	—
Horizon V (upper)	2	3.06	3.26	3.45	—	3	1.01	1.19	1.30	—
Kannondo Cave Site										
Horizon unknown	8	2.88	3.01	3.18	0.09	8	1.09	1.20	1.33	0.08
Horizon I	15	2.40	2.93	3.32	0.22	15	1.01	1.19	1.31	0.09
Horizon J	7	2.52	2.94	3.26	0.25	7	0.98	1.16	1.25	0.10
LATE PLEISTOCENE										
Suse Quarry(East Fissure)** 1	—	—	2.98	—	—	1	—	1.18	—	—
Kumaishi-do Cave										
Site unknown	9	2.62	2.71	2.86	0.09	10	0.96	1.01	1.10	0.04
F ₃ , F ₂ and F ₄	30	2.49	2.76	3.25	0.17	32	0.93	1.06	1.16	0.05
F ₃	33	2.48	2.71	2.95	0.13	35	0.91	1.04	1.15	0.06
Kannondo Cave Site										
Horizon M (upper)	168	2.40	2.89	3.40	0.19	208	0.86	1.15	1.33	0.09
Horizon M (lower)	13	2.72	2.93	3.15	0.12	16	0.96	1.18	1.31	0.08
Horizon N	38	2.38	2.82	3.15	0.17	55	0.79	1.12	1.32	0.09
Horizon O (upper)	40	2.60	2.89	3.24	0.13	54	0.98	1.12	1.29	0.08
Horizon O (lower)	14	2.83	2.92	3.06	0.08	14	0.93	1.09	1.21	0.08
Horizon P	12	2.66	2.82	2.95	0.09	15	0.89	1.10	1.20	0.07
Seiryukutsu Cave	1	—	3.18	—	—	1	—	1.12	—	—
Yage Quarry**										
Site 1	2	2.78	2.93	3.09	—	2	0.93	1.10	1.27	—
Site 2	1	—	3.03	—	—	1	—	1.14	—	—
Site 4	2	2.60	2.66	2.72	—	2	0.99	1.02	1.05	—
Site 5	3	2.76	2.81	2.89	—	3	1.07	1.10	1.12	—
Sugi-ana Cave	39	2.41	2.76	3.29	0.19	43	0.91	1.02	1.19	0.08
Aisawa Quarry	5	2.75	2.91	3.12	0.14	5	1.11	1.13	1.29	0.09
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	1	—	2.82	—	—	2	1.21	1.23	1.24	—
Loc.3 of Ube Kosan Quarry										
Horizon unknown	1	—	2.59	—	—	1	—	1.08	—	—
Layer 18	5	2.57	2.63	2.69	0.05	5	1.05	1.11	1.15	0.03
Layer 17	2	2.64	2.75	2.86	—	2	1.09	1.10	1.11	—
Layer 14	4	2.59	2.63	2.72	—	6	0.93	0.99	1.07	0.05
Layer 13	11	2.53	2.77	2.88	0.10	11	0.99	1.05	1.16	0.06
Layer 12	7	2.68	2.88	3.07	0.13	7	0.92	1.09	1.18	0.08
Layer 10	5	2.73	2.81	2.94	0.08	5	1.04	1.14	1.19	0.06
Layer 9	2	2.70	2.77	2.83	—	2	1.15	1.18	1.21	—
Layer 8	7	2.52	2.80	2.99	0.15	9	1.01	1.12	1.25	0.07
Layer 6	2	2.70	2.75	2.80	—	2	1.07	1.07	1.08	—
Layer 4	5	2.60	2.85	3.17	0.19	5	0.93	1.11	1.20	0.10
Layer 1	1	—	3.00	—	—	1	—	1.26	—	—

Table 69. Measurements of M_2 of *Microtus montebelli* in mm. * KANAMORI Collection; ** MATSUHASHI Collection; ○ Grid B-1. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	m	min	m	max	SD	m	min	m	max	SD
RECENT MATERIALS										
Karumai	6	1.42	1.53	1.63	0.07	6	0.93	0.99	1.05	0.04
Sugadaira*	74	1.36	1.54	1.84	0.10	74	0.81	1.00	1.18	0.08
Kurehayama	1	—	1.57	—	—	1	—	0.96	—	—
Mikawa Heights	22	1.54	1.53	1.75	0.06	22	1.01	1.07	1.15	0.04
HOLOCENE										
Anagami Site (Layer 4)°	1	—	1.62	—	—	1	—	1.03	—	—
Kannondo Cave Site										
Horizon unknown	3	1.51	1.58	1.62	—	3	0.97	1.00	1.02	—
Horizon I	8	1.50	1.63	1.85	0.12	8	0.98	1.09	1.19	0.06
Horizon J	4	1.43	1.53	1.62	—	4	0.84	0.97	1.06	—
LATE PLEISTOCENE										
Suse Quarry (East Fissure)**	1	—	1.60	—	—	1	—	1.01	—	—
Kannondo Cave Site										
Horizon 0 (upper)	4	1.54	1.59	1.66	—	4	0.86	0.96	1.07	—
Horizon 0 (lower)	3	1.51	1.62	1.73	—	3	0.90	1.02	1.08	—
Yage Quarry **										
Site 1	1	—	1.73	—	—	1	—	1.09	—	—
Site 2	1	—	1.73	—	—	1	—	1.01	—	—
Site 4	1	—	1.48	—	—	1	—	0.87	—	—
Site 5	3	1.53	1.54	1.55	—	3	0.92	0.94	0.96	—
Sugi-ana Cave	3	1.48	1.53	1.55	—	3	0.93	0.94	0.95	—
MIDDLE PLEISTOCENE										
Loc.3 of Ube Kosan Quarry										
Layer 18	1	—	1.47	—	—	1	—	1.02	—	—
Layer 14	1	—	1.49	—	—	1	—	0.91	—	—
Layer 13	4	1.41	1.49	1.59	—	4	0.87	0.92	0.96	—
Layer 12	2	1.58	1.59	1.60	—	2	0.95	0.96	0.96	—

Table 70. Measurements of M_3 of *Microtus montebelli* in mm. * KANAMORI Collection; ** MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
RECENT MATERIALS										
Karumai	6	1.45	1.56	1.70	0.10	6	0.72	0.84	0.94	0.08
Sugadaira*	74	1.22	1.49	1.78	0.12	74	0.63	0.82	1.00	0.09
Kurehayama	1	—	1.46	—	—	1	—	0.80	—	—
Mikawa Heights	22	1.36	1.57	1.68	0.08	22	0.80	0.88	0.95	0.04
HOLOCENE										
Suse Quarry**	1	—	1.46	—	—	1	—	0.83	—	—
Kannondo Cave Site										
Horizon J	1	—	1.24	—	—	1	—	0.63	—	—
LATE PLEISTOCENE										
Kannondo Cave Site										
Horizon 0 (upper)	—	—	—	—	—	1	—	0.80	—	—
Yage Quarry (Site 5)**	1	—	1.44	—	—	1	—	0.82	—	—
Sugi-ana Cave	1	—	1.51	—	—	1	—	0.74	—	—

the broadly confluent T4 with T5 like *Pitymys*. In the same illustration, "*forresti*" and "*irene*" show more simplified M³ than that of the present fossils. Moreover M₁ patterns of the two forms considerably differ from that of the present fossils in the number of closed triangles, the shape of anterior loop and the confluence of T4 with T5.

Microtus bedfordi is known only from the type locality in Kansu, China. This species is very peculiar in having grooved incisors, extremely simplified M³ (with only two closed triangles and a very small posterior loop) and only four closed triangles in M₁ (THOMAS, 1911a; HINTON, 1926; CORBET, 1978). None of these characters are observed in any specimens of the present fossils.

Microtus brandtii now occurs in Mongolia and Transbaikalia. According to the descriptions and illustrations of TOKUDA (1941b) and OGNEV (1950), M³ of this species is much simpler than that of the present fossils. Namely its posterior loop is small and simplified so that only three salient angles are observed on both sides, and LRA4 is undeveloped. Five closed triangles are present in M₁ of both *M. brandtii* and present fossils. However the shape of the anterior loop is quite different from each other. That of *M. brandtii* is small and squarish in shape, and characterized by the absence of LRA5 and BRA4 (LRA5 sometimes present but very faint). An additional character of the mandible of *M. brandtii* was stated by TOKUDA (1941b); namely the area between the ascending ramus and alveolus is not deeply pocketed, but becomes a shallow groove as in *Clethrionomys*. This character is not visible in the present fossils.

The Late Pleistocene remains of *M. brandtii* were described by TOKUDA (1939) from Ku-hsiang-tung, Northeast China, although he considered that *M. brandtioides*, a fossil species proposed by YOUNG (1934), was conspecific to this species. TOKUDA's illustration (Text-fig. 8) evidently shows that M₁ of these remains are considerably different from those of the present Japanese fossils. The remains of *M. brandtii* were also reported from several "Lower Pleistocene" localities in Transbaikalia (AGADJANIAN and ERBAJEVA, 1983). They are easily discriminated from the present fossils both in M³ and M₁ patterns (see their Fig. 40).

The range of *M. mandarinus* is restricted to North China and Korea. The molar patterns of this species resemble those of *M. brandtii*; namely M³ with very simple triangular posterior loop, and M₁ with five closed triangles and a small quadrate anterior loop. Therefore the present Japanese fossils are distinct from this species by the same characters as those of *M. brandtii*.

M. fortis is more extensively distributed than the other East Asiatic species of *Microtus*. It ranges from Central China to Northeast China, Korea and Transbaikalia. *M. fortis* is generally larger in size than the other East Asiatic *Microtus* including the present fossils. OGNEV (1950) stated that M³ of this species carried four and three salient angles on the lingual and buccal sides respectively, and the fourth supplementary salient angle on the buccal face of the posterior loop was frequently observed. In addition to these descriptions, OGNEV's figure (Fig. 117) indicates that the M³ pattern of *M. fortis* is similar to that of the present fossils in having the C- or F-shaped posterior loops. M₁ of *M. fortis* is characterized by the presence of five closed triangles and by the anterior loop with distinctive LSA5 and with smoothed buccal wall (absence of BSA4). Therefore M₁ of this species is readily distinguishable from that of the present fossils. These dental characters were also described by TOKUDA (1941b) in which he

treated this species as *M. pelliceus* THOMAS. Moreover, in the figure of HINTON (1926, Fig. 40), the same characters are observable in *M. calamorum* THOMAS which is generally included in *M. fortis* (ELLERMAN and MORRISON-SCOTT, 1951; CORBET, 1978).

The fossils of *M. fortis* are recorded from the Late Pleistocene Ku-hsiang-tung (TOKUDA, 1939) and the Middle Pleistocene Tologoi (only in a list, VANGENGEM and SHER, 1970). According to TOKUDA, the former fossils are represented by only two isolated M_1 and referred to *M. cf. pelliceus*. They share the characters with the living *M. fortis*, and are therefore easily distinguishable from the present Japanese fossils by their larger size and the shape of the anterior loop of M_1 .

M. clarkei is distributed in Yunnan (South China) and North Burma. Its molar patterns are well illustrated by HINTON (1926, Fig. 41). As CORBET (1978) described, this species is characterized by a postero-lingual extra ridge in M^2 , four lingual salient angles in M^3 (consequently posterior loop C-shaped), and six lingual and five buccal salient angles in M_1 . The shapes of M^3 and M_1 are rather similar to those of the present fossils, but that of M^2 is decidedly different.

M. millicens is known only from Szechuan, China. In accordance with THOMAS (1912a), the molar pattern of this species is unique in having a well-developed postero-lingual extra angle in M^2 and four closed triangles in M_1 . Moreover T2 and T3 are united in M^3 , and T3 and T4 are also united in M_2 . None of these characters are present in the molars of the present fossils.

M. kikuchii is now restricted in distribution to the high mountains of Taiwan. The descriptions and illustrations of its molars were given by KURODA (1920), AOKI and TANAKA (1941), TOKUDA (1941b) and KANEKO (1987). Judging from them, the size is somewhat larger than that of the present fossils. The F-shaped posterior loop of M^3 which sometimes appears in the present fossils is also observed in *M. kikuchii*. M_1 of *M. kikuchii* has five closed triangles as that of the present fossils, but the shape of the anterior loop is somewhat different between them. In M_1 of *M. kikuchii*, LRA4 deeply intrudes into the anterior loop, whereas both LRA5 and BRA4 are less developed than in the present fossils. Additionally, the well-developed BSA3 and BRA2 of M_3 were considered to be characteristic features of *M. kikuchii* by TOKUDA (1941b), but such characters are not observed in the present fossils.

M. mongolicus occurs both in Mongolia and in Transbaikalia. This species is sometimes treated as a subspecies of *M. arvalis* (OGNEV, 1950; ELLERMAN and MORRISON-SCOTT, 1951). *M. mongolicus* carries M^3 with the C-shaped posterior loop as the present fossils. On the other hand, there are five closed triangles in M_1 , but its anterior loop is rather simple than that of the present fossils. The morphological variation of M_1 is shown in OGNEV's illustrations (Figs. 95 and 97 in OGNEV, 1950). The smoothed buccal wall of the anterior loop (namely lack of conspicuous BSA4 and BRA4) seems to be frequently observed in this species. In some specimens, however, BSA4 and BRA4 seem to be developed in various degrees as in the figures of TOKUDA (1941b) and OGNEV (1950).

The Late Pleistocene fossils comparable to *M. mongolicus* were reported from Ku-hsiang-tung (TOKUDA, 1939). Almost all the specimens illustrated by him (Text-fig. 15) possess

well-developed BSA4 and BRA4 in M_1 , and therefore these specimens are quite similar to the present Japanese fossils.

M. sachalinensis is known only from Sakhalin. According to VASIN (1955), M^3 of this species has very complicate pattern in which six closed fields are formed. The posterior loop is divided into two closed fields by the constriction between the bottoms of LRA4 and BRA4. Such a pattern is never observed in the present fossils, although M_1 pattern is rather similar to each other.

*M. maximowiczii** distributed in Transbaikalia seems to be somewhat larger in size than the present fossils. M^3 pattern of this species is quite similar to that of the present fossils in having mainly C- or F-shaped posterior loops and rarely E-shaped one (OGNEV, 1950). OGNEV also described the variation in M_1 pattern. M_1 with five closed triangles is most frequently observed, but in rare case T6 is completely closed. The shape of the anterior loop is generally similar to that of the present fossils in having well-developed LSA5 and BSA4 (plus LRA5 and BRA4). Therefore, as far as the dental morphology is concerned, *M. maximowiczii* is considered to be most closely related to the present fossils and living *M. montebelli* among the above-mentioned East Asiatic species.

Comparisons with other living species —

The following species are now extensively distributed from Europe to Siberia:

Microtus oeconomus (PALLAS, 1776)

Microtus agrestis (LINNAEUS, 1761)

Microtus gregalis (PALLAS, 1779)

Microtus arvalis (PALLAS, 1779)

Additionally, *M. middendorffi* (POLIAKOV, 1881) is known only from the northern extremities of Siberia. According to CORBET (1978), *M. hyperboreus* can be treated as conspecific with this species.

M. oeconomus and *M. agrestis* are easily separable from the present fossils by the number of closed triangles in M_1 and by the presence of the postero-lingual extra angle in M^2 respectively.

M. gregalis is distinct from other species of *Microtus* by its characteristic narrow skull. In this species, the posterior loop of M^3 is usually C- or F-shaped like the present fossils, but sometimes upside-down L-shaped (OGNEV, 1950, Fig. 213). Although M_1 constantly possesses five closed triangles (rarely six as figured by TOKUDA, 1941b), its anterior loop is highly variable in shape. The lack of BSA4 in the anterior loop is typical to this species (sometimes called "gregalid" type), but the well-developed BSA4 ("arvalid" type) is also frequently observed. Moreover there exists a series of intermediate forms between these two types. The analyses of the living and Late Quaternary fossil populations by NADACHOWSKI (1982) indicate that the frequency of each type seems to be changeable in accordance with geological age and locality. Such kinds of variation can not be found in the present fossils and in the living *M. montebelli*, in

* Recently two allied species to *M. maximowiczii* were found in Eastern Siberia. One is *M. evoronensis* from the lower reach of the Amur River (KOVALSKAYA and SOKOLOV, 1980). Another is *M. mujanensis* from northeast of Lake Baikal (ORLOV and KOVALSKAYA, 1978). Their molar patterns are very similar not only to *M. maximowiczii* but also to *M. montebelli*.

which the "gregalid" type and several intermediate forms never occur.

The Late Pleistocene fossil of *M. gregalis* was described by TOKUDA (1939) from Ku-hsiang-tung. Its M_1 pattern with six closed triangles and a squarish anterior loop is dissimilar to the typical pattern of *M. gregalis* as well as the present Japanese fossils. In addition to these characters, the size of the Ku-hsiang-tung specimen is somewhat smaller than the present fossils.

M. middendorffi has somewhat more complicate M^3 than the present fossils; namely four salient angles on both lingual and buccal sides, and occasional presence of LSA6 and BRA4 (OGNEV, 1950). OGNEV also illustrated the constriction in the posterior loop of M^3 which is observed between the bottoms of LRA4 and BRA4. This constriction is never found in the present fossils. M_1 of *M. middendorffi* has five closed triangles as that of the present fossils. In *M. middendorffi*, however, the anterior loop is more variable in shape than that of the present fossils.

The fossils of *M. middendorffi* (including *M. hyperboreus*) are known from the "Upper and Middle Pleistocene" of East Siberia (AGADJANIAN and ERBAJEVA, 1983). Judging from their figures (Figs. 23 and 32), these fossils are easily distinguished from the present Japanese fossils by the shape of the anterior loop of M_1 .

The molar pattern of the living *M. arvalis* is quite similar to that of the present fossils. Its variation on the living materials from U.S.S.R. was described by OGNEV (1950). He recognized the following four morphotypes in M^3 in accordance with Rörig and Börner (1905):

1. "Forma typica"; four salient and three re-entrant angles present on the lingual side, but three salient and two re-entrant angles on the buccal side.
2. "Forma duplica"; an additional salient angle (BSA4) developed on the buccal side; consequently four salient and three re-entrant angles present on this side.
3. "Forma variabilis"; five salient and four re-entrant angles present on the lingual side; but four salient and three re-entrant angles on the buccal side.
4. "Forma simplex"; three salient and two re-entrant angles present on both sides.

The "forma typica" seems to correspond to the morphotypes C_1 , F_1 , BC_1 and BF_1 proposed by the present author. This type is most frequently found in the living population of *M. arvalis*. The "forma duplica" possibly corresponds to the morphotypes C_2 , F_2 , BC_2 and BF_2 of the present author. This type is extremely rare in the living *M. arvalis*. The "forma variabilis" equivalent to the morphotype E of the present author is also rare. The "forma simplex" probably corresponding to the morphotypes R_1 and R_2 of the present author is rarely found (3–5%). Such frequencies of each morphotype are well coincident with those of the present fossils as well as the living *M. montebelli* analysed in the present study.

In regard to M_1 , the most typical pattern of *M. arvalis* illustrated by OGNEV (1950) is equivalent to the most frequent pattern of the present fossils. NADACHOWSKI (1982) analysed the detailed variation of M_1 pattern of *M. arvalis* collected from Poland. His materials comprised not only recent specimens but also the Late Quaternary fossils which were assigned to *M. cf. arvalis*. Ten morphotypes (A to J) were proposed by him to classify these materials. NADACHOWSKI's morphotype A is characterized by the poorly developed BSA4 and LRA5. This morphotype does not occur in the living population of *M. arvalis*, but is very rarely found

in its fossil populations. Such a pattern is also invisible in the present Japanese fossils and the living *M. montebelli*. In his morphotype B, BSA4 is well developed, while BRA4 is absent. Judging from his figure (Fig. 15), this morphotype is somewhat similar to the morphotype R of the present author. The frequency of the morphotype B in *M. arvalis* (ca. 2–3%) approximates to that of the morphotype R in the present Japanese fossils (ca. 2–3%). NADACHOWSKI's morphotype C and D are possibly equivalent to the normal morphotypes such as O, I₁, I₂ and A of the present author in having well-developed LSA5, LRA5, BSA4 and BRA4. NADACHOWSKI noted that 87–96% of the specimens of *M. arvalis* belonged to his morphotypes C and D. The percentages in the Japanese materials are similar (91–98%). His morphotype E is characterized by the well-developed LSA6 and inconspicuous BSA5. This type is very rarely found in *M. arvalis* (0.2–2.1%), but never occurs in the Japanese materials. In his morphotype F, the anterior loop is more complicate than in E. Namely BSA5 and LRA6 are weakly developed there. This morphotype is also rare in *M. arvalis* (0.4–2.6%), and never observed in the Japanese materials. His morphotypes G and H are characterized by the strong constriction between the bottoms of LRA5 and BRA4. Judging from his figure (Fig. 15), T6 and T7 are opposite in position and broadly confluent with each other. Although these morphotypes are rarely found in *M. arvalis* (2–8%), none of the Japanese materials belong to them. His morphotype I possibly corresponds to the morphotype Act of the present author, in which six closed triangles are formed and the constriction between the bottoms of LRA5 and BRA4 is not so strong as in the above-mentioned G and H. This morphotype is very rarely observed in the fossil populations of *M. arvalis* (1.4%), but the frequency in the Japanese materials are somewhat higher (6–7%). His morphotype J with six closed triangles and with the strong constriction between the bottoms of LRA5 and BRA4 is also rare in *M. arvalis* (0.4%), although it is not found in the Japanese materials.

These detailed comparisons reveal that *M. arvalis* is quite similar to the living *M. montebelli* and present Japanese fossils not only in the general molar patterns but also in the frequencies of each morphotype. Such similarity is much higher than that to *M. agrestis* and *M. gregalis*.

M. arvalinus HINTON, a fossil species closely related to *M. arvalis* and *M. agrestis*, is known from the Middle Pleistocene of Europe, although CHALINE (1972) synonymized it with *M. arvalis*. In accordance with SUTCLIFFE and KOWALSKI (1976), this species is identical in its M₁ pattern with the living *M. arvalis*/*M. agrestis* group, but differs only in its slightly smaller dimensions. Such circumstances are also observed in the Japanese fossils where the Middle Pleistocene form is generally slightly smaller than the Late Pleistocene and Holocene ones as well as the recent *M. montebelli* (Tables 66–70).

Comparisons with the Chinese fossil species —

The following three species have been hitherto described from the Middle and Late Pleistocene of China, although some authors discussed the validity of these species (TOKUDA, 1939 etc.):

Microtus epiratticeps YOUNG, 1934

Microtus brandtioides YOUNG, 1934

Microtus complicitens PEI, 1936

They are easily distinguishable by the number of closed triangles in M_1 . Namely, four, five and six closed triangles are present in *M. epiratticeps*, *M. brandtioides* and *M. complicitens* respectively. The present Japanese fossils with five closed triangles (rarely six) in M_1 correspond to *M. brandtioides* in this character only. However the shape of the anterior loop of M_1 is considerably different between them. According to YOUNG (1934) and PEI (1936), the anterior loop of *M. brandtioides* is simpler, and usually lacks BRA4 and well-developed BSA4. Only one variant illustrated by YOUNG (1934; 6 of Fig. 40) is somewhat similar to the present Japanese fossils, but this specimen belongs to a young individual as stated by YOUNG. Moreover M^3 of *M. brandtioides* is much simpler than that of the present fossils. In *M. brandtioides*, the posterior loop of M^3 is very small and sub-rectangular in shape so that LSA5 and LRA4 are lacking.

M. complicitens is known from two localities of Choukoutien (Loc. 3 and Loc. 15). PEI's illustrations (1936; Figs. 35 and 36) indicates that the M^3 and M_1 patterns of this species are different from the typical patterns of the present Japanese fossils, although they are similar to the patterns of the minor variants of the latter (morphotypes E and Act in M^3 and M_1 respectively).

The fossil assemblage of *Microtus* collected from the Latest Pleistocene sediments of the Upper Cave of Choukoutien was studied by PEI (1940). Although he reserved the definite specific determination of these materials, he described the variation of their M^3 and M_1 patterns in detail. In M^3 , his type I with C- or F-shaped posterior loops is equivalent to the morphotypes C₁ and F₁ of the present author. This type is commonly found in the Upper Cave assemblage, and should be identified as *M. epiratticeps*, if the definition by YOUNG (1934) is valid. PEI's type II is much simpler and corresponds to M^3 of YOUNG's *M. brandtioides*. This type is not found in the present Japanese fossils.

In regard to M_1 of the Upper Cave assemblage, PEI distinguished the type I from II by the number of closed triangles; namely the former four, but the latter five. The type I corresponding to YOUNG's *M. epiratticeps* is very rarely found in the assemblage. The type II was subdivided into four types mainly by the shape of the anterior loop. Among them, the type IIa with well-developed LSA5 and faint LSA6 is somewhat similar to the M_1 pattern of *M. fortis*, although the buccal wall of the anterior loop is not so smoothed as in *M. fortis*. The type IIb (especially IIb₁, IIb₂ and IIb₃) is quite similar to the present Japanese fossils in having well-developed LSA5 and BSA4 (consequently LRA5 and BRA4 are formed). The type IIc with almost closed T6 bears a resemblance to *M. complicitens* and the extreme variant of the present Japanese fossils (the morphotype Act). The type IId with small and round anterior loop is somewhat similar to M_1 of *M. brandtii* and *M. mandarinus*. PEI stated the frequencies of each morphotype in the Upper Cave assemblage as follows: IIa rather uncommon, IIb rather common, IIc relatively rare and IId very common.

On the basis of his observations, PEI discussed the difficult problem about the classification of the Upper Cave *Microtus*. He mentioned "if the lower jaws are all (except IId) referred to a same form (which should be *M. brandtioides*...), then what about the lower jaws corresponding to the upper jaws of *epirratticeps* or type I?" and "if, on the other hand, lower jaws of type I are ... referred to *M. epiratticeps*, how to explain that in the Upper Cave three mandibles only of type I

have been found, whereas the upper teeth of type I are so numerous?" On the contrary to PEI's opinion, the present author is convinced that M_1 is more important than M^3 in the classification of fossil *Microtus* as many palaeontologists have been regarded, and *M. epiratticeps* is separable from *M. brandtioides* by the morphology of M_1 .

In the provisional view of the present author, the *Microtus* assemblage of the Upper Cave seems to comprise more than three species. The types I and II d of M_1 probably represent *M. epiratticeps* (or *M. oeconomus*) and *M. brandtioides* (or *M. brandtii*) respectively*. The type II b of M_1 may be referred to some allied form to *M. montebelli*. Moreover the type II a and II c may belong to some different species. If such interpretations are correct, the type I of M^3 (*epiratticeps* type) corresponds to M_1 with the patterns of the type I (*epiratticeps* type) as well as of the type II b (*montebelli* type). Therefore the frequent occurrence of the type I in M^3 can be explained as the mixture of *M. epiratticeps* and some allied form to *M. montebelli*.

Concluding remarks on the comparisons —

In conclusion, the present Japanese fossils are most similar to *M. maximowiczii* and *M. arvalis* among the above-mentioned living species of *Microtus*, as far as the molar patterns are concerned. The molar patterns of *M. maximowiczii* and *M. arvalis* are almost indistinguishable from that of the living *M. montebelli*. The recent distributions of these three species are isolated from each other; namely Transbaikalia of *M. maximowiczii*, Europe to Western Siberia of *M. arvalis* and Japan of *M. montebelli* (Fig. 147). From such distributions and other geological and palaeontological evidences, it is most reasonable that the present fossils are assigned to *M. montebelli* rather than *M. maximowiczii* and *M. arvalis* as already mentioned.

The affinity of *M. montebelli* to the living continental species has been discussed by several authors. The following species have been considered as the allied species to *M. montebelli*:

1. *Microtus oeconomus* by TOKUDA (1941b), IMAIZUMI (1949) and MIYAO (1970).
2. *M. arvalis* by ELLERMAN and MORRISON-SCOTT (1951), TOKUDA (1969) and KOWALSKI and HASAGAWA (1976).
3. *M. maximowiczii* by ZIMMERMANN (1964)**.
4. *M. maximowiczii* and *M. mongolicus* by CHALINE (1974b).

The close relationship to *M. oeconomus* is untenable from its dental characters and some palaeontological evidences, although YAMAKAGE *et al.* (1985) insisted the close relationship between *M. montebelli* and *M. oeconomus* from the banding patterns on chromosomes. Other opinions are acceptable from the viewpoint of the present author.

Almost all the fossils of *Microtus* described from China are distinct from the present fossils of *M. montebelli* in molar pattern. Exceptionally, the similarity to *M. montebelli* is observed only in two examples. One is type II b of M_1 in the *Microtus* assemblage of the Upper Cave. Another is "*M. cf. mongolicus*" from Ku-hsiang-tung. These two records are assigned to the later period of the Late Pleistocene.

* II d in PEI's illustration (Fig. 21-d) resembles M_1 of European *M. nivalis* rather than that of East Asiatic *M. brandtii*, as far as the shape of the anterior loop is concerned.

** ZIMMERMANN treated *M. fortis* as a subspecies of *M. maximowiczii*, and included *M. kikuchii* as well as *M. montebelli* in his "*M. maximowiczii* Gruppe."

Discussion

Microtus montebelli is now the only representative of the genus *Microtus* in Japan. It is considered to be an endemic species to Japan. It usually inhabits in grasslands or cultivate fields (especially alluvial plains) as other species of *Microtus*, but is sometimes found in parklands or even in forests. In the present Japanese Islands, its distribution is restricted to Honshu, Kyushu and Sado Island, whereas it is unknown from Hokkaido, Shikoku and the Ryukyu Islands. SOKOLOV (1954) reported the occurrence of this species from Shikotan Islands of the Southern Kurile Islands. As KANEKO (1975) pointed out, this record is quite doubtful. In Honshu, this species is densely distributed in the north-eastern part, but becomes sparse south-westward. Moreover it is relatively rare in Kyushu (KISHIDA, 1924; KURODA, 1940; IMAIZUMI, 1960; MIYAO, 1970). Corresponding to the scarcity in southwest Honshu and Kyushu, the fossils of this species are relatively few in the Holocene localities of these areas. However they are more abundantly found in the Late Pleistocene localities of the same areas. This fact suggests that this species probably decreased in the period from the Late Pleistocene to Early Holocene there.

It is rather curious that *Microtus montebelli* is now absent from Shikoku, because this big island is separated from Honshu and Kyushu only by the narrow and shallow inland sea called the Seto Inland Sea where hundreds of islands are studded. Almost all the areas of this inland sea were undoubtedly emerged in the cold periods of the Late Pleistocene. In the present Shikoku, the habitats which the preference of *M. montebelli* is expected are occupied by other murid and arvicolid such as *Apodemus speciosus* and *Phaulomys smithii* (KANEKO, 1972; 1979; 1982).

The author is convinced that *Microtus montebelli* inhabited in Shikoku at least in the Late Pleistocene, although the reliable fossil record of this species is lacking in this island*. The reasons for saying this are (1) the abundant occurrence of this species from the Late Pleistocene localities in the adjacent areas, and (2) the reliable land connection among Shikoku, Honshu and Kyushu in this period. The absence of the fossil record probably depends on the extreme scarcity of the micro-mammalian fossil localities in Shikoku, and on the lack of the detailed studies on the fossil micro-mammals of the island.

It is inferred that during the Late Pleistocene, *M. montebelli* inhabited in Shikoku, especially in the vast alluvial plains which were existent in the areas of the present Seto Inland Sea. In the period between the Latest Pleistocene and Early Holocene, the climatic and vegetational conditions were drastically changed, so that the preferable habitats of this species were mostly destroyed. Moreover the above-mentioned vast alluvial plains were submerged to be the inland sea. Consequently *M. montebelli* was extremely diminished in number from Shikoku, and thus was thoroughly extinguished by the competition with the other murid or arvicolid.

The absence of *M. montebelli* in Hokkaido can be explained that the Tsugaru Strait between Honshu and Hokkaido avoided the invasion of this species into Hokkaido during the Late Pleistocene. The preferable habitats for *M. montebelli* are mostly occupied by *Clethrionomys*

* See KANEKO, Y. (1975, 1982). The record of *M. montebelli* from Early Holocene Kamikuroiwa Site (KANEKO, H., 1967) is doubtful.

rufocanus in the present Hokkaido, which is a different species from *C. japonicus* known from the Pleistocene of Honshu. The Tsugaru Strait is much deeper than the Seto Inland Sea, and several recent authors tend to deny the Late Pleistocene land connection between Honshu and Hokkaido even in the coldest phase, although this problem is still controversial. Moreover the present study suggests that the micro-mammalian faunal exchange through this strait did not occur during the Late Pleistocene. It is also inferred that *M. montebelli* did not inhabit in Hokkaido in other periods than the Late Pleistocene. Unfortunately, since the micro-mammalian fossils are unknown from Hokkaido, this hypothesis can not be assured by any fossil evidences. From the viewpoint of the present author, there are no bases for the immigration of this species through Sakhalin and Hokkaido to Honshu which was stated by MIYAO (1970). The affinity of *M. montebelli* to *M. oeconomus* is questionable as already mentioned, and the abundant occurrence of *M. montebelli* in the present northeast Honshu does not indicate the immigration route from Hokkaido to Honshu, but possibly results from the fact that large alluvial plains present in this area even in Postglacial time have guaranteed the suitable habitats to this species.

The absence of this species from the Ryukyu Islands is readily explained. The land connection between the islands and Kyushu has not been expectable since the Early Pleistocene. Moreover the climatic and vegetational conditions of the islands are considerably different from those of the main land of Japan during all the periods of the Quaternary. Therefore there have been no preferable habitats to *M. montebelli* in the islands.

M. montebelli is absent from the middle Middle Pleistocene localities in Japan such as Ikumo and Ando Quarries, where *M. epiratticepoides* and *M. cf. brandtioides* are exclusively found. The oldest records of *M. montebelli* are those from Localities 1 and 3 of Ube Kosan Quarry which are dated as the late Middle Pleistocene. The close alliance to *M. arvalis* indicates that *M. montebelli* was probably originated from *M. arvalis* or some Middle Pleistocene ancestral form of *M. arvalis* group. The evolutionary history of *M. arvalis* in Europe has been studied by several authors (CHALINE, 1966; 1972; 1974b; FEJFAR and HORÁČEK, 1983 and others). This species was possibly derived from *Microtus (Allophaiomys) pliocaenicus* in the early Middle Pleistocene of Europe, and then spread eastward. When it reached Eastern Siberia, it probably branched into several groups (*M. maximowiczii*, *M. mongolicus* etc.). One of these groups possibly shifted south-eastward into Northeast China to be some ancestral form of *M. montebelli* in the middle Middle Pleistocene. In this period, it did not invade into North China, but migrated into Japan via the Korean Peninsula in the late Middle Pleistocene (Fig. 147). The fossil records from the Upper Cave of Choukoutien and Ku-hsiang-tung probably suggest that some allied forms to *M. montebelli* barely survived until the Latest Pleistocene in Northeast China and its adjacent area. These forms might be the descendants of the ancestral form of *M. montebelli* in the continent.

In Locality 3 of Ube Kosan Quarry, the fossils of *M. montebelli* are rarely obtained from the lower layers, but increase in number toward the upper layers. Moreover, in the Late Pleistocene localities of Honshu, it becomes much more abundant than the precedent inhabitants such as *M. epiratticepoides* and *M. cf. brandtioides*. This fact indicates that the predominancy

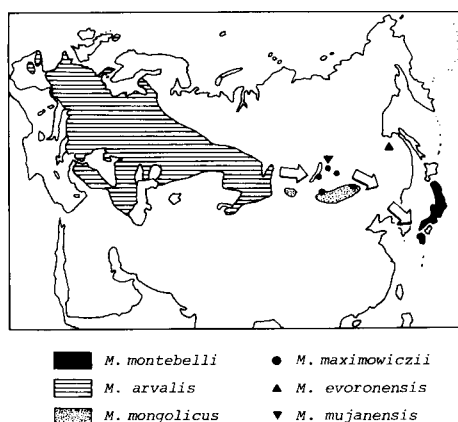


Fig. 147. Suggested immigration route of *Microtus montebelli* or its ancestor. The recent distributions of the allied species are also illustrated. They are mainly based on CORBET (1978).

in the *Microtus* population of Japan was replaced from *M. epiratticepoides* to *M. montebelli* in some period between the late Middle Pleistocene and Late Pleistocene. The environmental change since the late Middle Pleistocene permitted such replacement within the *Microtus* population, because new environmental conditions were more suitable for *M. montebelli* than the precedent inhabitants.

During the Late Pleistocene, the land connection seems to have interrupted between the main part of Japan (Honshu, Kyushu and Shikoku) and the Korean Peninsula as well as between the former and Hokkaido. Under such isolated conditions, *M. montebelli* could not invade into Hokkaido. After the precedent inhabitants, *M. epiratticepoides* and *M. cf. brandtioides*, had been completely extinguished in the Latest Pleistocene, *M. montebelli* became the only representative of *Microtus* in Japan. As the climate became warmer from the Latest Pleistocene to Early Holocene, *M. montebelli* decreased in number in southwest Honshu and Kyushu, and was thoroughly extinguished from Shikoku.

***Microtus epiratticepoides*, sp. nov.**

(Figs. 148–152; Pls. 24–26)

Synonym —

Microtus montebelli montebelli; NAORA 1954, *Old Stone Age in Japan*, 128 (Fig. 80); from Matsugae Cave.

Microtus epiratticeps YOUNG; KOWALSKI and HASEGAWA 1976 (in part), *Bull. Nat. Sci. Mus. Ser. C*, **2**, 57–61; from Ikumo Quarry, Ando Quarry, Shiriya Quarry and Shiraiwa Mine.

Microtus epiratticeps YOUNG; HASEGAWA *et al.* 1976 (in part), *Quat. Res. (Daiyonki-kenkyu)*, **16**, 14–15; from Ando Quarry.

Microtus cf. epiratticeps YOUNG; KAWAMURA 1977, *Fossil Club Bull.*, (14), 7; from Kumaishi-do Cave.

Microtus epiratticeps YOUNG; KAWAMURA and KAJIURA 1980 (in part), *Jour. Speleol. Soc. Japan*, **5**, 62–63; from Sugi-ana Cave.

Microtus epiratticeps YOUNG; KAWAMURA 1981, 1982, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, **4**, 69, 81–82; **5**, 60; from the Late Pleistocene horizons of Kannondo Cave Site.

Microtus epiratticeps YOUNG; OKUMURA *et al.* 1982 (in part), *Earth Sci.*, **36**, 216; from Kumaishi-do Cave.

Microtus cf. epiratticeps YOUNG; KAWAMURA *et al.* 1986, *Ann. Bull. Hiroshima Univ. Taishaku-kyo Sites Res. Centre*, 9, 71; from the Late Pleistocene horizons of Kannondo Cave Site.

Holotype — Right isolated M^3 (KUJC96094) from Layer 17 of Locality 3 of Ube Kosan Quarry.

Paratypes — Right mandible with I , M_1 and M_2 (KUJC97038) from Layer 4 of Locality 3 of Ube Kosan Quarry, and left isolated M^3 (ASM 700001) from Layer 2 of the same locality.

Referred materials —

MIDDLE PLEISTOCENE LOCALITIES

Locality 4 of Ube Kosan Quarry

1 skull fragment with left M^1 – M^2 and right M^1 – M^3 (ASM 701401).

Locality 3 of Ube Kosan Quarry

Layer 1: 5 isolated M^3 (KUJC96017, 96019, 96020, 96024, 96026); 1 mandible with M_1 and M_2 (KUJC96008); 1 mandible with M_1 (KUJC96007); 20 isolated M_1 (KUJC96002–96005, 96009–96016, 96021–96023, 97052–97056).

Layer 2: 1 isolated M^3 (KUJC96037); 1 mandible with I and M_1 (KUJC97059); 1 mandible with M_1 (KUJC96027); 16 isolated M_1 (KUJC96028–96030, 96032, 96035, 96036, 97057, 97058, 97060–97067).

Layer 3: 4 isolated M^3 (KUJC96049, 96052–96054); 15 isolated M_1 (KUJC96038–96047, 97068–97072).

Layer 4: 5 isolated M^3 (KUJC96062–96066); 2 mandibles with I and M_1 – M_3 (KUJC97073, 97075); 9 mandibles with I , M_1 and M_2 (KUJC97076, 97077, 97079–97085); 2 mandibles with M_1 and M_2 (KUJC97074, 97078); 2 mandibles with I and M_1 (KUJC97091, 97092); 2 mandibles with M_1 (KUJC97120, 97121); 39 isolated M_1 (KUJC96056–96061, 97086–97090, 97093–97119, 97122).

Layer 5: 4 isolated M_1 (KUJC96172–96175).

Layer 6: 4 isolated M^3 (KUJC96262–96264, 96266); 7 isolated M_1 (KUJC96252–96258).

Layer 8: 4 isolated M^3 (KUJC96157, 96159, 96162, 96169); 2 mandibles with I , M_1 and M_2 (KUJC97141, 97142); 24 isolated M_1 (KUJC96134–96145, 96154, 96156, 97139, 97140, 97143–97150).

Layer 9: 8 isolated M^3 (KUJC96122–96128, 96131); 1 mandible with I and M_1 (KUJC97136); 2 mandibles with M_1 (KUJC96112, 97134); 13 isolated M_1 (KUJC96113–96120, 97132, 97133, 97135, 97137, 97138).

Layer 10: 2 isolated M^3 (KUJC96108, 96109); 1 mandible with I and M_1 (KUJC97126); 11 isolated M_1 (KUJC96099–96102, 97124, 97125, 97127–97131).

Layer 11: 2 isolated M^3 (KUJC96249, 96250); 1 mandible with I , M_1 and M_2 (KUJC96248); 2 isolated M_1 (KUJC96246, 96247).

Layer 12: 5 isolated M^3 (KUJC96239–96242, 96245); 1 mandible with M_1 and M_2 (KUJC96228); 1 mandible with M_1 (KUJC96225); 5 isolated M_1 (KUJC96226, 96227, 96229, 96237, 96238).

Layer 13: 1 isolated M^3 (KUJC96212); 2 isolated M_1 (KUJC96198, 96199).

Layer 14: 1 isolated M^3 (KUJC96193); 7 isolated M_1 (KUJC96177–96183).

Layer 16: 1 isolated M_1 (KUJC96098).

Layer 17: 2 isolated M^3 (KUJC96092, 96093); 5 isolated M_1 (KUJC96086–96088, 96096, 97123).

Layer 18: 1 isolated M^3 (KUJC96073); 5 isolated M_1 (KUJC96070–96072, 96075, 96081).

Horizon unknown: 3 isolated M^3 (KUJC96268, 96269, 96272); 1 mandible with I , M_1 and M_2 (KUJC96267); 3 isolated M_1 (KUJC96270, 96271, 96274).

Locality 1 of Ube Kosan Quarry

1 isolated M^3 (ASM 701402) and 1 isolated M_1 (ASM 701403) from Layer 4; 2 isolated M_1 from Layer 3 (ASM 701404, 701405); 3 isolated M^3 (ASM 701406–701408) and 8 isolated M_1 (ASM 701409–701416) from Layer 2; 1 isolated M_1 from Layer 1 (ASM 701417).

LATE PLEISTOCENE LOCALITIES

Locality 2 of Ube Kosan Quarry

1 isolated M_1 (ASM 701418).

Sugi-ana Cave

5 isolated M^3 (KUJC100165–100169), 15 isolated M_1 (KUJC100170–100184).

Yage Quarry (unnumbered specimen of the MATSUHASHI Collection)

1 isolated M_1 from Site 1.

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

Horizon P: 3 isolated M_1 (K03729–03731).

Horizon O (lower part): 4 isolated M^3 (K03732–03735); 6 isolated M_1 (K03736–03741).

Horizon O (upper part): 16 isolated M^3 (K03742–03757); 16 isolated M_1 (K03758–03773).

Horizon N: 2 isolated M^3 (K03774, 03775); 2 isolated M_1 (K03776, 03777).

Horizon M (lower part): 2 isolated M_1 (K03778, 03779).

Kumaishi-do Cave

F₃: 2 isolated M^3 (YKS 04081, 04103).

F₄: 2 isolated M_1 (YKS 00081, 00085).

Origin of nomen — *epirratticepoides*, a compound word of *epi-ratticeps* and *ratticep-oides*, means a Japanese fossil species similar to the living *M. ratticeps* (= *oeconomus*) as well as to the fossil species such as the Chinese *M. epirratticeps* and the European *M. ratticepoides*.

Type locality — Locality 3 of Ube Kosan Quarry, Mine, Yamaguchi Prefecture, west Japan (131°13'37"E, 34°10'32"N).

Geological distribution — Middle to Late Pleistocene (extinguished between ca. 10,000 and 15,000 yr. B.P.)

Geographical distribution — Japan; hitherto known only from Honshu.

Diagnosis

M^3 with simplified posterior loop which is mostly upside-down L-shaped and sometimes very simple C-shaped; LSA5 undeveloped or poorly developed, so that Ls_5/Ls_4 is less than 0.45; the posterior loop broad, so that Wm/Ls_4 is mostly more than 1.0. M_1 with four closed triangles; Is 6 always open (isthmus index more than 2.0); degree of development of BSA4 variable.

Description

M^1 and M^2 —

The patterns of these molars are identical with those of other species of the Japanese *Microtus* which are described in p. 274.

M^3 —

The molar pattern is simpler than that of *M. montebelli*, but somewhat more complicate than that of *M. cf. brandtioides*. Three salient angles are observed on both lingual and buccal sides. The additional fourth salient angle on the lingual side (LSA5) is sometimes present, although it is much weaker than that of *M. montebelli*. Three re-entrant angles are also observed on both lingual and buccal sides. The most posterior re-entrant angles (LRA4 and BRA3) are much shallower than other re-entrant angles.

The posterior loop usually shows upside-down L-shape, or sometimes simple C-shape. Ls_5/Ls_4 is usually less than 0.40 in relation to the poorly developed LSA5. The main part of the posterior loop is relatively broad and short. Consequently, Wm/Ls_4 is mostly more than 1.0, and the length of the posterior loop (Lp) mostly ranges between 30% and 40% of the total occlusal length of the crown (Fig. 139). LSA4 distinctly projects lingually from the main part to form a distinct embayment (LRA4), even if LSA5 is absent. The buccal wall of the posterior loop is usually smoothed, so that the formation of BSA4 is very rare.

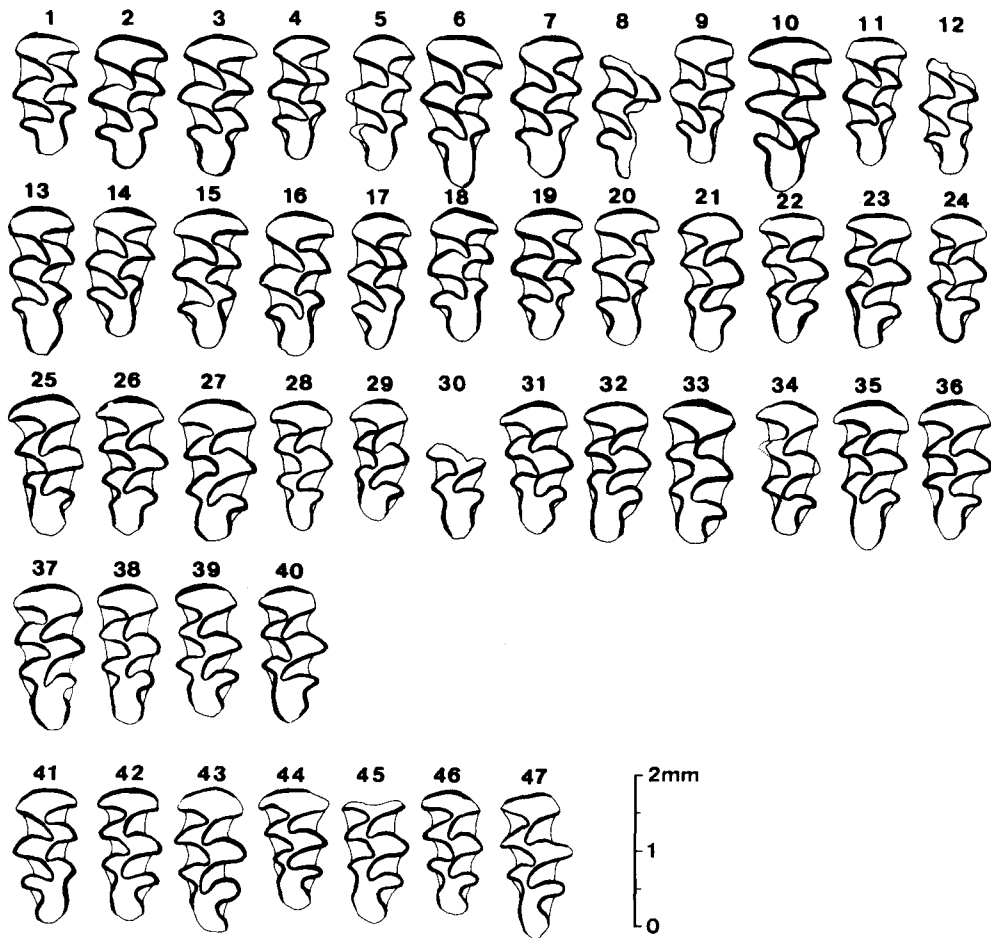


Fig. 148. Isolated M^3 of *Microtus epiratticepoides*, sp. nov. from Locality 3 of Ube Kosan Quarry (1–20, 41, left M^3 ; 21–40, 42–47, right M^3).

1, KUJC96019 from Layer 1; 2, ASM 700001 from Layer 2 (paratype); 3, 4, KUJC96062 and 96063 from Layer 4; 5, 6, KUJC96262 and 96264 from Layer 6; 7, 8, KUJC96157 and 96169 from Layer 8; 9–11, KUJC96122, 96123 and 96125 from Layer 9; 12, KUJC96092 from Layer 17; 13, KUJC96017 from Layer 1; 14, KUJC96263 from Layer 6; 15, KUJC96272 (horizon unknown); 16, 17, KUJC96124 and 96126 from Layer 9; 18, KUJC96239 from Layer 12; 19, KUJC96049 from Layer 3; 20, KUJC96268 (horizon unknown); 21, 22, KUJC96024 and 96026 from Layer 1; 23–25, KUJC96065, 96066 and 96064 from Layer 4; 26, KUJC96266 from Layer 6; 27, 28, KUJC96159 and 96162 from Layer 8; 29, 30, KUJC96108 and 96109 from Layer 10; 31–33, KUJC96240–96242 from Layer 12; 34, KUJC96212 from Layer 13; 35, 36, KUJC96093 and 96094 (holotype) from Layer 17; 37, KUJC96020 from Layer 1; 38, KUJC96127 from Layer 9; 39, KUJC96250 from Layer 11; 40, KUJC96193 from Layer 14; 41, KUJC96249 from Layer 11; 42, KUJC96037 from Layer 2; 43, 44, KUJC96052 and 96054 from Layer 3; 45, 46, KUJC96128 and 96131 from Layer 9; 47, KUJC96245 from Layer 12.

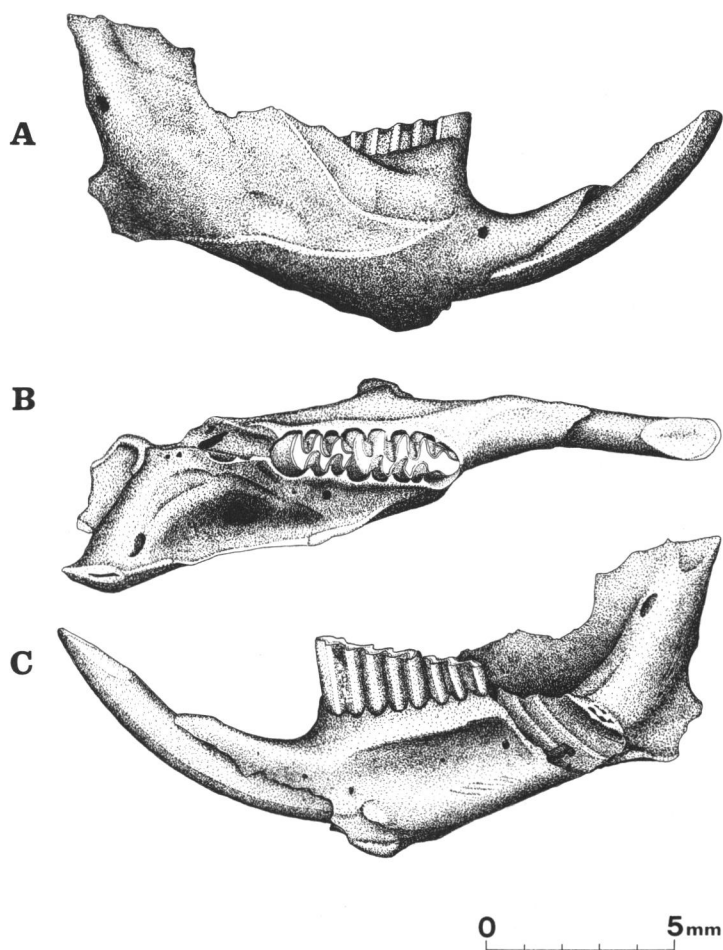


Fig. 149. Right mandible with I, M_1 and M_2 of *Microtus epiratticepoides* sp. nov. from Layer 4 of Locality 3 of Ube Kosan Quarry (paratype; KUJC97038).

A, buccal view; B, upper view; C, lingual view.

Mandible —

The general characters of the mandible are coincident with the generic characters of the Japanese *Microtus*. The position of the mandibular foramen is "arvalis type" of HALL and YALDEN (1978).

M_1 —

The molar pattern is similar to that of *M. oeconomus*. Is 1 to Is 5 are always closed, whereas Is 6 is always open. The isthmus index is mostly more than 3.0, but rarely 2.0 to 3.0. Consequently four closed triangles are formed between the anterior and posterior loops. Five salient and five re-entrant angles are observed on the lingual side, although the most anterior

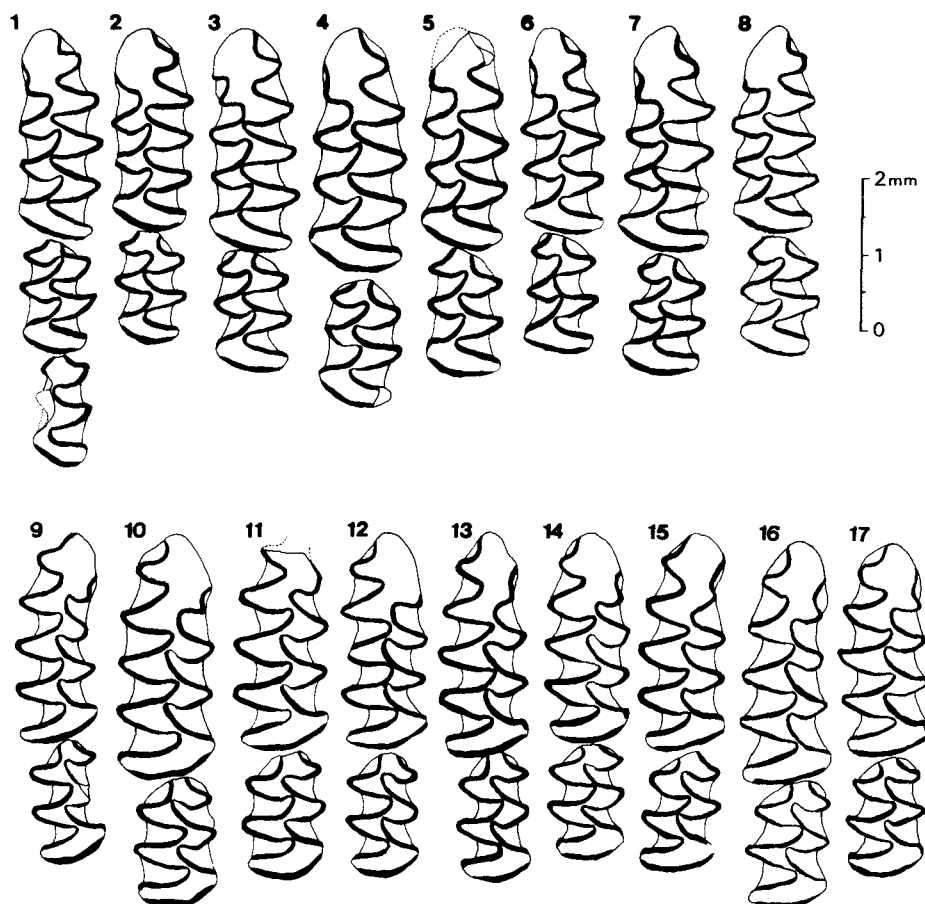


Fig. 150. Lower tooth rows of *Microtus epiratticepoides*, sp. nov. from Locality 3 of Ube Kosan Quarry. The specimens with broader Is 6 in M_1 (isthmus index more than 3.0) are figured.

1, left M_1 – M_3 from Layer 4 (KUJC97075); 2–8, left M_1 and M_2 from Layer 4 (KUJC97077, 97076, 97079–97082, 97074 respectively); 9, right M_1 and M_2 from Layer 1 (KUJC96008); 10–12, right M_1 and M_2 from Layer 4 (KUJC97083–97085 respectively); 13, right M_1 and M_2 from Layer 4 (paratype, KUJC97038); 14, right M_1 and M_2 from Layer 12 (KUJC96228); 15, right M_1 and M_2 , horizon unknown (KUJC96267); 16, right M_1 and M_2 from Layer 4 (KUJC97078); 17, right M_1 and M_2 from Layer 11 (KUJC96248).

re-entrant angle (LRA5) is much shallower than others, or sometimes absent. On the other hand, three or four salient angles and re-entrant angles are also observed on the buccal side. The degree of the development of the most anterior salient angle (BSA4) and re-entrant angle (BRA4) is highly variable. In nearly half of the examined specimens, the buccal wall of the anterior loop is smoothed without BSA4 and BRA4. The specimens with well-developed BSA4 and BRA4 are sometimes found, but their BSA4 and BRA4 are not so strong as those of *M. montebelli*.

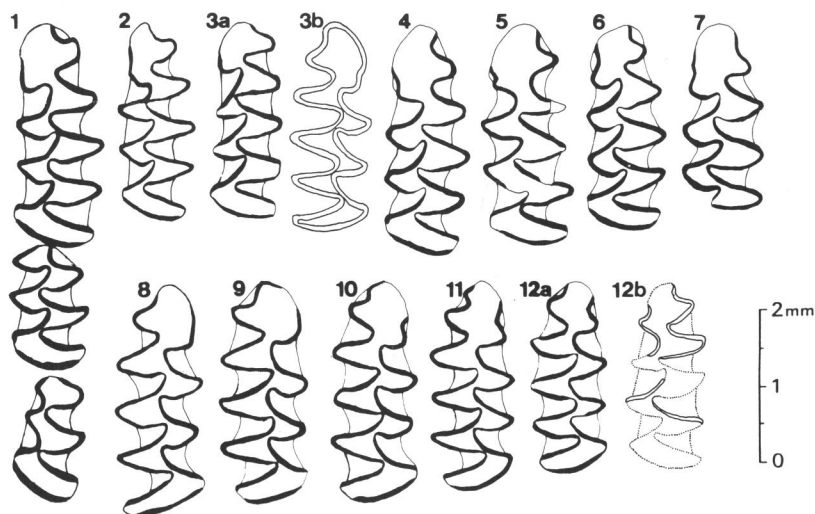


Fig. 151. *Microtus epiratticepoides*, sp. nov. from Locality 3 of Ube Kosan Quarry. The specimens with narrower I_s 6 in M_1 (isthmus index less than 3.0 but more than 2.0) are figured. 1, left M_1 – M_3 ; 2–7, left isolated M_1 ; 8–12, right isolated M_1 .

1, KUJC97073 from Layer 4; 2, KUJC96086 from Layer 17; 3, KUJC96175 from Layer 5 (3a, occlusal view; 3b, bottom view); 4, KUJC96038 from Layer 3; 5, KUJC96070 from Layer 18; 6, KUJC96061 from Layer 4; 7, KUJC96088 from Layer 17; 8, KUJC96011 from Layer 1; 9, 10, KUJC96154 and 96139 from Layer 8; 11, KUJC96060 from Layer 4; 12, KUJC96002 from Layer 1 (12a, occlusal view; 12b, bottom view).

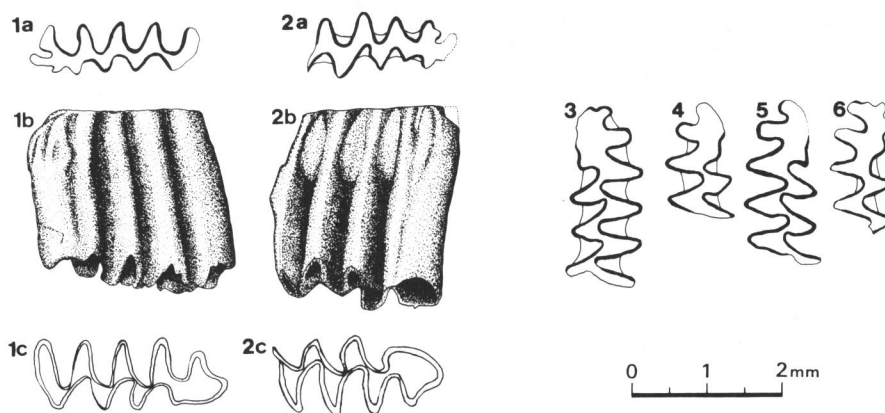


Fig. 152. Isolated M_1 of young individuals of *Microtus epiratticepoides*, sp. nov. from Locality 3 of Ube Kosan Quarry (1, 3, left M_1 ; 2, 4, 5, 6, right M_1).

1, KUJC96043 from Layer 3 (1a, occlusal view; 1b, buccal view; 1c, bottom view); 2, KUJC96081 from Layer 18 (2a, occlusal view; 2b, buccal view; 2c, bottom view); 3, KUJC96096 from Layer 17; 4, KUJC96032 from Layer 2; 5, KUJC96087 from Layer 17; 6, KUJC96156 from Layer 8.

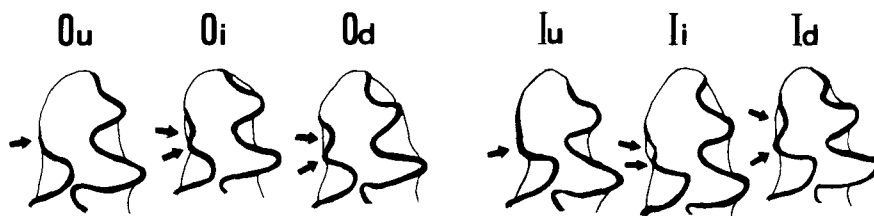


Fig. 153. Morphotypes of M_1 of *Microtus epiratticepoides*, sp. nov. The anterior loop is exclusively figured. Arrows indicate the degree of the development of BRA4 (upper) and BSA4 (lower). For detailed explanation of each morphotype see text.

M_1 of younger individuals exhibit somewhat different patterns from those of the above-mentioned full-grown specimens. Six young specimens are available for description (Fig. 152). The following characters are observed in common:

Indentation distinctly appears on the anterior wall of the anterior loop. All the isthmuses tend to be open, so that each dentine field is confluent, but Is 6 is relatively broader than other isthmuses. The shape of the anterior loop is rather complicate. LSA6 and LRA5 are well-developed, and BSA4 forms a distinct angle. Such a shape resembles some variants of *Microtus malei* HINTON described by CHALINE (1972; Fig. 53, 54), but is not found in the full-grown specimens of the present fossils.

M_2 and M_3 —

These molars have the same characters as those given in p. 274 as the generic characters of the Japanese *Microtus*.

Morphological analysis of molars

The morphological variation of M_1 is examined here. All the fossil specimens can be divided into the following six morphotypes in accordance with the isthmus index and the degree of the development of BSA4 (Fig. 153):

1. Open type: Namely Is 6 is widely open, so that the isthmus index exceeds 3.0.
 - Morphotype Ou*: Open type with no trace of BSA4. The buccal wall of the anterior loop is smoothed without any projection.
 - Morphotype Oi*: Open type with slightly developed BSA4. The degree of the development of BSA4 is intermediate between the morphotypes Ou and Od.
 - Morphotype Od*: Open type with developed BSA4. However BSA4 is less developed than that of *M. montebelli*.
2. Intermediate type: Namely Is 6 is narrower than the above-mentioned open type, but broader than those of *M. montebelli* and *M. cf. brandtioides*. The isthmus index ranges between 2.0 and 3.0.
 - Morphotype Iu*: Intermediate type without BSA4. This morphotype is a transitional form to *M. cf. brandtioides* in which Is 6 is completely closed (isthmus index less than 2.0).
 - Morphotype Ii*: Intermediate type with slightly developed BSA4. The degree of the development of BSA4 is intermediate between the morphotypes Iu and Id.
 - Morphotype Id*: Intermediate type with developed BSA4. This morphotype is a transitional form to *M. montebelli*. LRA5 and BRA4 are shallower than those of *M. montebelli*, so that the constriction of the anterior loop is not formed.

The number of the specimens belonging to each morphotype is shown in Table 71. The

Table 71. Frequency of each morphotype in M_1 of *Microtus epiratticepoides*, sp. nov. The number of the specimens belonging to each morphotype is shown. * MATSUHASHI Collection.

LOCALITY	M O R P H O T Y P E S O F M_1						TOTAL
	O_u	O_i	O_d	I_u	I_i	I_d	
LATE PLEISTOCENE							
Kumaishi-do Cave (F_4)	2	—	—	—	—	—	2
Kannondo Cave Site							
Horizon M (lower)	—	—	1	—	—	1	2
Horizon N	2	—	—	—	—	—	2
Horizon O (upper)	10	3	3	—	—	—	16
Horizon O (lower)	3	2	1	—	—	—	6
Horizon P	1	1	—	—	—	1	3
Yage Quarry (Site 1)*	—	—	1	—	—	—	1
Sugi-ana Cave	11	3	1	—	—	—	15
Loc.2 of Ube Kosan Quarry	1	—	—	—	—	—	1
MIDDLE PLEISTOCENE							
Loc.1 of Ube Kosan Quarry							
Layer 1	1	—	—	—	—	—	1
Layer 2	1	2	1	—	—	—	4
Layer 3	1	—	1	—	—	—	2
Layer 4	1	—	—	—	—	—	1
Loc.3 of Ube Kosan Quarry							
Horizon unknown	2	1	1	—	—	—	4
Layer 18	—	—	3	1	1	—	5
Layer 17	—	2	—	2	1	—	5
Layer 16	1	—	—	—	—	—	1
Layer 14	5	2	—	—	—	—	7
Layer 13	2	—	—	—	—	—	2
Layer 12	1	3	1	—	—	—	5
Layer 11	2	—	1	—	—	—	3
Layer 10	8	4	—	—	—	—	12
Layer 9	9	3	3	—	1	—	16
Layer 8	10	8	3	2	2	1	26
Layer 6	4	2	—	—	—	—	6
Layer 5	3	—	—	1	—	—	4
Layer 4	19	17	14	1	2	3	56
Layer 3	3	9	1	—	1	—	14
Layer 2	12	3	4	—	—	—	19
Layer 1	9	3	7	1	—	1	22

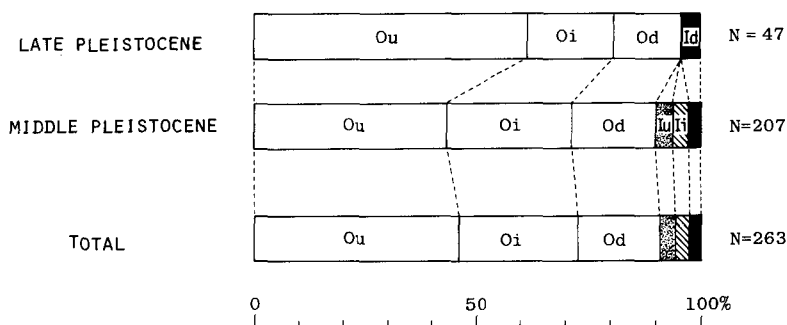


Fig. 154. Frequency of each morphotype in M_1 of *Microtus epiratticepoides*, sp. nov. The percentages are shown. "Late Pleistocene" and "Middle Pleistocene" comprise the data from four localities (Sugi-ana Cave, Yage Quarry, Kannondo Cave Site and Kumaishi-do Cave) and those from Locality 3 of Ube Kosan Quarry respectively. The data obtained from other localities are also included in "Total." N, number of specimens.

percentages of each morphotype are calculated and illustrated in Fig. 154.

The open type predominates in all the localities (totally 91%). Among the subdivisions of this type, the morphotype Ou is most abundant. Its percentage against the total number of specimens attains to 46% as a whole. In the Late Pleistocene localities, it is enhanced to be 62%. In the Middle Pleistocene locality (Locality 3 of Ube Kosan Quarry), however, it is somewhat lower (42%). The morphotypes Oi and Od are rather few (26 and 18% respectively).

The intermediate type sometimes appears in the populations of this species (totally 9%). The morphotypes Iu and Ii are considerably scarce in the Middle Pleistocene locality (3% each), but absent from the Late Pleistocene localities. The frequency of the morphotype Id is also very low (3%). This morphotype is, however, found in both Middle and Late Pleistocene localities.

Measurements

The measurements of the mandibles and molars are given in Tables 72–75.

Comparisons

M_1 of the present fossils are characterized by four closed triangles and the perfect separation of T4 from T5. In regard to the former character, the species of the subgenera *Allophaiomys*, *Phaiomys* (*sensu* CHALINE, 1974b) and *Pedomys* are easily distinguishable from the present fossils in having only three closed triangles. Furthermore, such Eurasian species of *Microtus* as *M. brandtii*, *M. mandarinus*, *M. fortis*, *M. kikuchii*, *M. mongolicus*, *M. sachalinensis*, *M. maximowiczii*, *M. gregalis*, *M. agrestis*, *M. arvalis* and *M. montebelli* are clearly distinct from the present fossils in having five closed triangles in M_1 . As for the latter character of the present fossils, the species of the subgenus *Pitymys* (*sensu stricto*) differ from them in having broadly confluent T4 with T5.

Table 72. Measurements of the mandibles of *Microtus epiratticepoides*, sp. nov. from Locality 3 of Ube Kosan Quarry in mm. The numbers on the left side correspond to those in Fig. 72.

	Horizon unknown	Layer 12	Layer 10	Layer 9			Layer 8		Layer 4			
	KUJC 96267	KUJC 96228	KUJC 97126	KUJC 96112	KUJC 97134	KUJC 97136	KUJC 97141	KUJC 97142	KUJC 97073	KUJC 97074	KUJC 97075	KUJC 97076
1. Total length of the mandible (id to goc)	—	—	—	—	—	—	—	—	—	—	—	—
4. Length of the horizontal ramus	—	—	—	—	—	—	—	—	10.66±	—	—	—
5. Length of the diastema	—	—	—	3.85±	3.47±	3.95±	3.70±	4.02±	4.10±	3.92	—	4.03
6. Length of the ascending ramus (M ₂ to the condyle)	—	—	—	—	—	—	—	—	—	—	6.99	—
7. Ditto (M ₂ to goc)	—	—	—	—	—	—	—	—	—	—	4.67	—
8. Height of the ascending ramus (gov to the condyle)	—	—	—	—	—	—	—	—	—	—	7.71	—
10. Ditto (gov to the mandibular incision)	—	—	—	—	—	—	—	—	—	—	5.89	—
12. Maximum height of the horizontal ramus	4.01	3.66	3.71	3.87	3.46	3.87	3.64	3.96	3.86	—	3.64	3.72±
13. Height of the horizontal ramus behind M ₂	—	—	—	—	—	—	—	—	2.78±	—	—	—
14. Maximum thickness of the horizontal ramus	3.15	3.10	3.05	3.00	3.00	3.15	2.95	2.90	2.97	—	3.10	2.96
15. Length of the molar row (M ₁ to M ₂) at the crowns	—	—	—	—	—	—	—	—	6.24	—	5.77	—
16. Ditto at the alveoli	—	—	—	—	—	—	—	—	6.63±	—	6.01	—
17. Length of the molar row (M ₁ to M ₂) at the crowns	4.54	4.34	—	—	—	—	4.30±	4.48	4.51	4.36	4.30	4.43
18. Ditto at the alveoli	4.69	4.66	4.55±	—	—	4.92	4.60	4.72	4.50	4.56	4.38	4.79

	Layer 4												Layer 2		Layer 1	
	KUJC 97077	KUJC 97078	KUJC 97079	KUJC 97080	KUJC 97081	KUJC 97082	KUJC 97083	KUJC 97084	KUJC 97085	KUJC 97038	KUJC 97091	KUJC 97092	KUJC 97120	KUJC 97059	KUJC 96007	KUJC 96008
1.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15.86
4.	—	10.82±	—	—	—	—	—	—	—	—	—	—	—	—	—	—
5.	4.11	3.80±	4.10±	—	4.11	—	—	—	—	3.96±	3.96	4.40	—	3.67±	3.95	4.52
6.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12.	3.50	3.94	3.92	3.93	3.60	3.84	3.95	4.01	3.96	3.80	3.63±	3.81	3.62	3.77	3.92	3.64
13.	—	2.15±	—	—	—	—	—	—	—	—	—	—	—	—	—	—
14.	2.86	2.99	3.45	2.91	2.88	3.12	3.35	3.44	3.09	3.26	2.82	3.37	—	3.07	2.92	3.01
15.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
16.	—	7.07±	—	—	—	—	—	—	—	6.40±	—	—	—	—	—	—
17.	4.11	4.83	4.90	—	4.30	4.57	4.97	—	4.53	4.54	—	—	—	—	—	4.36
18.	4.23	4.99	—	4.74	4.37	4.79	4.95	4.82	4.74	4.66	—	4.80±	—	4.85	4.44	4.37

Table 73. Measurements of M^3 of *Microtus epiratticepoides*, sp. nov. in mm. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
LATE PLEISTOCENE										
Kumaishi-do Cave (F_3)	2	1.81	1.83	1.85	—	2	0.87	0.87	0.88	—
Kannondo Cave Site										
Horizon N	2	1.82	1.84	1.85	—	2	0.90	0.95	1.00	—
Horizon O (upper)	11	1.76	1.91	2.29	0.16	11	0.82	0.97	1.11	0.09
Horizon O (lower)	3	1.85	1.95	2.07	—	3	0.95	1.01	1.05	—
Sugi-ana Cave	5	1.57	1.78	1.92	0.13	5	0.85	0.94	1.00	0.05
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 2	3	1.76	1.83	1.87	—	3	0.90	0.92	0.93	—
Loc.3 of Ube Kosan Quarry										
Horizon unknown	3	1.67	1.77	1.84	—	3	0.87	0.91	0.97	—
Layer 18	1	—	2.04	—	—	1	—	1.03	—	—
Layer 17	2	1.84	1.91	1.98	—	2	0.96	0.98	1.00	—
Layer 14	1	—	1.82	—	—	1	—	0.87	—	—
Layer 13	1	—	1.73	—	—	1	—	0.87	—	—
Layer 12	5	1.75	1.85	1.92	0.07	5	0.90	0.96	1.02	0.04
Layer 11	2	1.76	1.78	1.80	—	2	0.83	0.85	0.87	—
Layer 10	1	—	1.62	—	—	1	—	0.82	—	—
Layer 9	7	1.70	1.85	2.04	0.11	7	0.79	0.88	1.10	0.11
Layer 8	3	1.71	1.82	1.90	—	3	0.78	0.93	1.06	—
Layer 6	4	1.70	1.84	2.03	—	4	0.91	0.97	1.08	—
Layer 4	5	1.62	1.77	1.88	0.13	5	0.79	0.90	1.01	0.09
Layer 3	4	1.60	1.75	1.91	—	4	0.87	0.92	0.94	—
Layer 2	2	1.76	1.77	1.78	—	2	0.85	0.90	0.96	—
Layer 1	5	1.60	1.81	1.94	0.13	5	0.86	0.90	0.94	0.03

The above-mentioned characters of the present fossils are found in M_1 of the following living species:

Microtus bedfordi (THOMAS, 1911)

Microtus millicens THOMAS, 1911

Microtus oeconomus (PALLAS, 1776)

Among these three species, however, *M. bedfordi* is readily distinguishable from the present fossils by somewhat simpler anterior loop in M_1 and only two closed triangles in M^3 . The grooved upper incisors characteristic to *M. bedfordi* are never found in any fossil population of the Japanese *Microtus*. *M. millicens* is discriminated from the present fossils by the united triangles in M^3 and M_2 , and by the presence of the postero-lingual extra ridge in M^2 .

In comparison with *M. bedfordi* and *M. millicens*, *M. oeconomus* is rather similar to the present fossils in molar pattern. This species is extensively distributed from Europe to Eastern Siberia, especially in the boreal part of the continent. OGNEV (1950) described the variation in molar pattern of the living *M. oeconomus* collected from U.S.S.R. According to him, M_1 pattern of this species is considerably similar to that of the present fossils, although he also recorded that M_1

Table 74. Measurements of M_1 of *Microtus epirallicepoides*, sp. nov. in mm. * MATSUHASHI Collection. Abbreviations as in Table 38.

LOCALITY	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
LATE PLEISTOCENE										
Kumaishi-do Cave (F ₄)	2	2.92	2.93	2.94	—	2	1.15	1.18	1.20	—
Kannondo Cave Site										
Horizon M (lower)	2	2.92	2.93	2.95	—	2	1.21	1.23	1.25	—
Horizon N	2	2.76	2.83	2.90	—	2	1.07	1.14	1.21	—
Horizon O (upper)	11	2.71	2.98	3.21	0.15	13	1.12	1.21	1.30	0.05
Horizon O (lower)	5	2.80	2.99	3.23	0.16	5	1.08	1.21	1.30	0.08
Horizon P	3	2.69	2.82	2.94	—	3	1.07	1.09	1.14	—
Yage Quarry (Site 1)*	1	—	3.00	—	—	1	—	1.19	—	—
Sugi-ana Cave	13	2.22	2.66	3.02	0.24	13	0.86	1.07	1.25	0.10
Loc.2 of Ube Kosan Quarry	1	—	2.92	—	—	1	—	1.16	—	—
MIDDLE PLEISTOCENE										
Loc.1 of Ube Kosan Quarry										
Layer 1	—	—	—	—	—	1	—	1.21	—	—
Layer 2	1	—	2.77	—	—	6	1.00	1.10	1.14	0.06
Layer 3	2	2.85	2.95	3.06	—	2	1.18	1.20	1.21	—
Layer 4	—	—	—	—	—	1	—	1.23	—	—
Loc.3 of Ube Kosan Quarry										
Horizon unknown	4	2.55	2.78	3.00	—	4	1.02	1.10	1.16	—
Layer 18	3	2.73	2.95	3.23	—	3	1.00	1.14	1.24	—
Layer 17	2	2.60	2.87	3.13	—	2	1.03	1.09	1.15	—
Layer 14	5	2.59	2.69	2.83	0.01	5	0.98	1.08	1.17	0.07
Layer 13	1	—	2.56	—	—	1	—	1.02	—	—
Layer 12	6	2.58	2.80	3.02	0.14	7	1.09	1.15	1.20	0.04
Layer 11	3	2.69	2.86	3.10	—	3	1.14	1.16	1.19	—
Layer 10	11	2.59	2.79	3.04	0.15	12	1.08	1.15	1.23	0.05
Layer 9	13	2.65	2.82	2.92	0.10	13	1.01	1.13	1.22	0.06
Layer 8	23	2.50	2.81	3.01	0.14	24	0.95	1.15	1.24	0.07
Layer 6	6	2.54	2.76	2.94	0.13	6	0.98	1.05	1.10	0.05
Layer 5	4	2.48	2.70	2.92	0.18	4	0.94	1.07	1.18	0.11
Layer 4	55	2.58	2.87	3.26	0.16	57	1.00	1.16	1.34	0.07
Layer 3	13	2.61	2.78	3.06	0.16	13	1.04	1.11	1.23	0.05
Layer 2	17	2.57	2.81	3.04	0.12	17	1.05	1.13	1.35	0.07
Layer 1	20	2.46	2.77	3.11	0.16	21	0.89	1.07	1.24	0.24

with five closed triangles were sometimes found. Recently, NADACHOWSKI (1982) analysed the detailed variation of M_1 in the Late Quaternary *M. oeconomus* as well as the living materials.

NADACHOWSKI's morphotypes (A–E) are fundamentally identical with the morphotypes proposed by the present author for the analyses of the present fossils. Judging from NADACHOWSKI's figure (Fig. 20), his morphotypes A, B, C₁ and C₂ correspond to the morphotype Ou of the present author which is characterized by the widely open Is 6 and the lack of distinct BSA4 and BRA4. His morphotype C₄ is possibly identical with the morphotype Oi of the present author, in which Is 6 is widely open, but BSA4 and BRA4 are slightly developed.

Table 75. Measurements of M_2 and M_3 of *Microtus epiratticepoides*, sp. nov. from Locality 3 of Ube Kosan Quarry in mm. Abbreviations as in Table 38.

TOOTH KIND AND HORIZON	L E N G T H					W I D T H				
	N	min	m	max	SD	N	min	m	max	SD
M_2										
Horizon unknown	1	—	1.55	—	—	1	—	1.06	—	—
Layer 12	1	—	1.54	—	—	1	—	1.05	—	—
Layer 11	1	—	1.57	—	—	1	—	1.08	—	—
Layer 8	2	1.59	1.62	1.66	—	2	1.06	1.06	1.07	—
Layer 4	14	1.50	1.65	1.72	0.07	14	0.92	1.05	1.11	0.05
Layer 1	1	—	1.62	—	—	1	—	0.97	—	—
M_3										
Layer 4	2	1.50	1.59	1.67	—	1	—	0.90	—	—

His morphotype D seems to be equivalent to the morphotype Iu of the present author which is characterized by narrower Is 6 and the lack of distinct BSA4 and BRA4. Although NADACHOWSKI stated that his morphotype E was characterized by the full separation of T5 from T6, his figure (Fig. 20, E₁–E₃) indicates that Is 6 is not so perfectly closed from the viewpoint of the present author's "isthmus index." Therefore this morphotype also corresponds to the morphotype Iu of the present author. As far as these morphotypes are concerned, the frequency of each morphotype in *M. oeconomus* comes near to that of each counterpart of the present fossils. On the other hand, the morphotypes Od, Ii and Id of the present author are not recorded in the populations of *M. oeconomus*. This fact indicates that BSA4 and BRA4 are less developed in *M. oeconomus* than in the present fossils.

The variation in M^3 pattern of *M. oeconomus* was also described in detail by OGNEV (1950). According to him, the posterior loop is mostly C- or F-shaped like that of *M. montebelli*. The upside-down L-shaped posterior loop characteristic to the present fossils seems to be rare in *M. oeconomus*. In conclusion, the differences between the present fossils and *M. oeconomus* are rather slight in M_1 pattern, but considerably great in M^3 pattern.

M. ratticepoides HINTON known from the Middle Pleistocene of Europe is considered to be the ancestor of *M. oeconomus* (SUTCLIFFE and KOWALSKI, 1976), although this species is sometimes treated as a synonym of *M. oeconomus* (for example, CHALINE, 1972). Judging from the descriptions and illustrations by HINTON (1923, 1926), HELLER (1930), BRUNNER (1934) and SUTCLIFFE and KOWALSKI (1976), the morphological difference in M_1 is rather slight between *M. ratticepoides* and *M. oeconomus* excepting the smaller size of the former. Therefore it can be said that the present Japanese fossils are also similar to *M. ratticepoides* in M_1 pattern. However the sufficient information on the M^3 pattern of *M. ratticepoides* is not available for the comparison with the present fossils.

M. nivalis (MARTINS, 1842) and several allied fossil species such as *M. nivaloides* MAJOR

1902, *M. nivalinus* HINTON 1923 and *M. malei* HINTON 1907 are closely related to *M. oecnomus* (CHALINE and MATTHEY, 1971; CHALINE, 1972, 1974b; FEJFAR and HORÁČEK, 1983). M^3 of the living *M. nivalis* has the simplified posterior loop which is mostly upside-down L-shaped in accordance with the descriptions of MILLER (1912), OGNEV (1950) and KOWALSKI (1957). Such M^3 pattern is nearly coincident with that of the present Japanese fossils.

M_1 pattern of both living and fossil *M. nivalis* is quite variable. It is typically characterized by five closed triangles, and by a small and round anterior loop. However the specimens with only four closed triangles or with more complicate anterior loop are frequently found. Although some variants of *M. nivalis* bear a resemblance to the present Japanese fossils, M_1 of *M. nivalis* is generally distinct from that of the present fossils.

M. nivaloides (including *M. nivalinus*) is known from the Middle Pleistocene of Europe, although CHALINE (1972) regarded it as a synonym of *M. nivalis*. According to the figure of HINTON (1926, Fig. 65), M_1 pattern of this species is subject to a wide range of variation. Such circumstances are also observed in *M. malei* (HINTON, 1907; CHALINE, 1972). In these species, some variants are quite similar to the present Japanese fossils, but others are dissimilar as in the above-mentioned *M. nivalis*. The M^3 patterns of these fossil species are not described in any literatures which are available to the present author.

Among the Chinese fossil species of *Microtus*, *M. brandtoides* and *M. complicitens* are readily distinguishable from the present Japanese fossils by the number of closed triangles in M_1 and by the shape of the posterior loop of M^3 . On the other hand, M_1 of *M. epiratticeps* resembles that of the present fossils in having four closed triangles. The variation of M_1 pattern of this species was described by YOUNG (1934) based on the materials from Locality 1 of Choukoutien. The M_1 pattern of *M. epiratticeps* is generally coincident with that of the present fossils, but some differences are also observable. In *M. epiratticeps*, the buccal wall of the anterior loop is mostly smoothed so that BSA4 is poorly developed and BRA4 is very rarely formed. This fact probably suggests that the morphotypes Oi, Od, Ii and Id by the present author are considerably scarce in the population of this species. This is also true in other records of *M. epiratticeps* from China*. The scarcity of these morphotypes is also observed in *M. oecnomus* as already discussed. In the present Japanese fossils, however, the frequency of these morphotypes is much higher, where it attains to 51% totally. Additionally, YOUNG (1934) stated that the posterior loop of M_1 was transversely set to the axis of the tooth row in *M. epiratticeps*. In the present fossils, however, it is rather obliquely set as in *M. brandtoides* described in the same paper.

The M^3 pattern of *M. epiratticeps* is decidedly different from the present Japanese fossils.

* The M_1 pattern of *M. epiratticeps* is observable in the figures of the following literatures:

1. PEI (1931) from Locality 5 of Choukoutien; originally assigned to *M. cf. brandti*.
2. PEI (1936) from Locality 3 of Choukoutien.
3. PEI (1940) from the Upper Cave of Choukoutien, originally assigned to *M. epiratticeps* (*M. brandtoides*).
4. ARCHAEOLOGICAL TEAM OF PROVINCIAL MUSEUM OF LIAONING and IVPP (1975) from Gezidong Cave.
5. HU and QI (1978) from Lantian.

According to the descriptions and illustrations by YOUNG (1934), its posterior loop is C-shaped with well-developed LSA5. Such a pattern is rather similar to that of the Japanese *M. montebelli*. As far as the present author observed the Choukoutien materials stored in the Institute of Vertebrate Palaeontology and Palaeoanthropology of Peking in 1983, he could not find any *Microtus* specimen with M^3 pattern similar to the Japanese fossils which were characterized by the upside-down L-shaped posterior loop. Namely the specimens labelled as *M. epiratticeps* and *M. brandtioides* had the C- or F-shaped posterior loop and very simplified posterior loop without LRA4 respectively.

It is concluded that the present Japanese fossils are possibly distinct from any living and fossils species of *Microtus* hitherto known from Eurasia. In regard to the M^3 pattern, they resemble *M. nivalis*, but the M_1 pattern is rather similar to *M. oeconomus* and *M. epiratticeps*. Therefore none of these species are coincident with the present fossils both in M^3 and M_1 patterns. Because the present author believes that these differences are sufficiently valuable for the specific distinction, he ventures to propose a new species named *M. epiratticepoides* for the Japanese fossils described here.

Discussion

KOWALSKI and HASEGAWA (1976) described a fossil form of *Microtus* other than *M. montebelli* from four localities in Japan such as Ikumo Quarry, Ando Quarry, Shiraiwa Mine and Shiriya Quarry. They regarded it as conspecific with the Chinese *M. epiratticeps*. Previously the present author followed their opinion. However the present study based on a large number of the additional materials has revealed that it should be divided into two forms, and both of them are not identifiable as *M. epiratticeps*. One form with four closed triangles in M_1 is regarded as the new species, *M. epiratticepoides*, and another with five closed triangles in M_1 is assigned to *M. cf. brandtioides*. The validity of such distinction is discussed in the subsequent section of *M. cf. brandtioides*.

KOWALSKI and HASEGAWA (1976) compared their "*M. epiratticeps*" with *M. oeconomus*, *M. nivalis*, *M. malei* and the Chinese *M. epiratticeps*. They concluded that their "*M. epiratticeps*" was most similar to the Chinese *M. epiratticeps* without any detailed explanation, although they recognized the differences in M^3 pattern. Because the detailed analyses of the molar patterns were not carried out by them, they underestimated the value of the characters of M^3 and M_1 peculiar to the present Japanese fossils. It is considered to be most probable that these differences in the molar patterns are sufficiently specific, because even slighter differences are sometimes regarded as specific in the living species of *Microtus*.

The occurrence of *M. epiratticepoides* from Ikumo Quarry is possibly the oldest record of this species in Japan, which is dated as the middle Middle Pleistocene. In China, the allied species, *M. epiratticeps*, appeared in the early or middle parts of the Middle Pleistocene (Lantian and the Layers 11 to 10 of Locality 1 of Choukoutien). These two species were possibly derived from the common ancestor of the latest Early or early Middle Pleistocene in China. This hypothetical ancestor might have the simplified M^3 like *M. epiratticepoides*, because the complication of M^3 pattern is assumed to be one of the general evolutionary trends in the genus

Microtus. In the continent, *M. epiratticeps* with complicate M^3 probably evolved from this ancestor to be an inhabitant of the temperate zone in North China, and survived until the Latest Pleistocene. On the other hand, a slight change probably occurred in the lineage from this ancestor to *M. epiratticepoides*. This ancestor might immigrate into Japan accompanying the temperate faunal elements of North China in the early Middle Pleistocene, and then evolved to be *M. epiratticepoides*. Until the late Middle Pleistocene, *M. epiratticepoides* was the leading species in the Japanese *Microtus* populations. After the invasion of *M. montebelli*, *M. epiratticepoides* was gradually surpassed by this new-faced species. During the Late Pleistocene, *M. epiratticepoides* decreased in number to be a minor species, and was completely extinguished at the end of this period.

The youngest records of this species are known from F₄ of Kumaishi-do Cave (¹⁴C age: ca. 17,000 yr. B.P.) and the lower part of Horizon M of Kannondo Cave Site (¹⁴C age: ca. 16,000 yr. B.P.). Therefore the time of the extinction is approximately estimated as 10,000 to 15,000 yr. B.P. In this time, the climatic and vegetational conditions were drastically changed in the Japanese Islands. The extinction possibly resulted from these environmental changes.

M. oeconomus which is rather similar to *M. epiratticepoides* in M_1 pattern is considered to be closely related to *M. nivalis* and *M. malei* (CHALINE and MATTHEY, 1971; CHALINE, 1972, 1974b). CHALINE proposed *M. malei burgondiae* as the common ancestor of these three species in the early Middle Pleistocene which was the descendant of the Early Pleistocene *Microtus* (*Allophaiomys*) *pliocaenicus*. *M. oeconomus* possibly arose in Europe or western Asia, and adapted to cold climate to spread eastward along the arctic and subarctic zones of the Eurasian Continent. Some authors pointed out the possibility that *M. epiratticeps* or even the allied Japanese form (*M. epiratticepoides* of the present author) were conspecific with *M. oeconomus* (TOKUDA, 1939; AIMI, 1974; HASEGAWA *et al.*, 1977). If the above-mentioned hypothesis is acceptable, such a possibility is rather unprobable. It is more probable that both *M. epiratticepoides* and *M. epiratticeps* belong to a separate lineage of East Asia from that of the above-mentioned *M. oeconomus* group of Europe, although the hypothetical ancestor of the East Asiatic group might evolve from the common stock to the ancestors of the *M. oeconomus* group.

Microtus cf. *brandtioides* YOUNG, 1934

(Figs. 155–158)

Synonym —

Microtus epiratticeps YOUNG; KOWALSKI and HASEGAWA 1976 (in part), *Bull. Nat. Sci. Mus.*, Ser. C, **2**, 57–61; from Ikumo Quarry and Shiraiwa Mine.

Microtus epiratticeps YOUNG; HASEGAWA *et al.* (in part), *Quat. Res. (Daiyonki-kenkyu)*, **16**, 14–15; from Ando Quarry.

Microtus epiratticeps YOUNG; KAWAMURA and KAJIURA 1980 (in part), *Jour. Speleol. Soc. Japan*, **5**, 62–63; from Sugi-ana Cave.

Microtus epiratticeps YOUNG; OKUMURA *et al.* 1982 (in part), *Earth Sci.*, **36**, 216; from Kumaishi-do Cave.

Microtus cf. *brandtioides* YOUNG; 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 LOCALITY****Locality 3 of Ube Kosan Quarry**

Layer 1: 2 isolated M^3 (KUJC96018, 96025).

Layer 4: 1 mandible with M_1 and M_2 (KUJC97153), 1 mandible with I and M_1 (KUJC96055), 1 isolated M_1 (KUJC97152).

Layer 6: 1 isolated M^3 (KUJC96265), 1 isolated M_1 (KUJC96252).

Layer 8: 3 isolated M^3 (KUJC96158, 96160, 96161), 4 isolated M_1 (KUJC96148, 96152, 96153, 97155).

Layer 9: 2 isolated M_1 (KUJC96121, 97154).

Layer 10: 2 isolated M^3 (KUJC96106, 96107).

Layer 18: 1 isolated M^3 (KUJC96082).

LATE PLEISTOCENE LOCALITIES**Sugi-ana Cave**

1 isolated M^3 (KUJC100185); 4 isolated M_1 (KUJC100186–100189).

Yage Quarry

1 isolated M_1 from Site 5 (unnumbered specimen of the MATSUHASHI Collection).

Kannonodo Cave Site

Horizon P: 1 isolated M_1 (HUA-K03780).

Horizon O (lower part): 1 isolated M^3 (HUA-K03781).

Horizon O (upper part): 2 isolated M^3 (HUA-K03782, 03783).

Horizon N: 1 isolated M_1 (HUA-K03784).

Horizon M (lower part): 2 isolated M_1 (HUA-K03785, 03786).

Kumaishi-do Cave

F₃: 1 mandible with I and M_1 (YKS 04005).

F₁, F₂ and F₄: 2 isolated M^3 (YKS 00277; 03013).

Diagnosis

M^3 with very simple posterior loop which is mostly sub-triangular in shape; LSA4 not differentiated from the main part of the posterior loop, so that LRA4 is not formed. M_1 with five closed triangles; both BSA4 and BRA4 mostly absent.

Description M^3 —

Three salient angles are observed on both lingual and buccal sides. The posterior loop is broad and short, and its length (Lp) mostly fluctuates between 29% and 37% of the total occlusal length of the crown (Fig. 139). It is generally sub-triangular in shape and thus

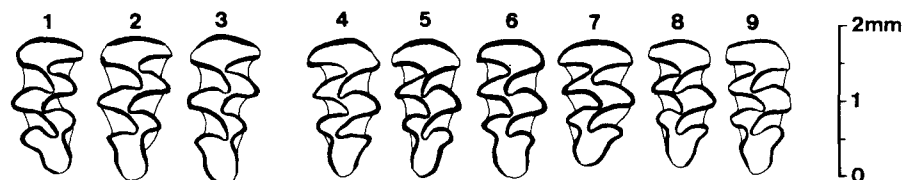


Fig. 155. Isolated M^3 of *Microtus* cf. *brandtioides* from Locality 3 of Ube Kosan Quarry (1–3, left M^3 ; 4–9, right M^3).

1, KUJC96018 from Layer 1; 2, 3, KUJC96107 and 96106 from Layer 10; 4, KUJC96025 from Layer 1; 5–7, KUJC96158, 96160, 96161 respectively from Layer 8; 8, KUJC96082 from Layer 18; 9, KUJC96265 from Layer 6.

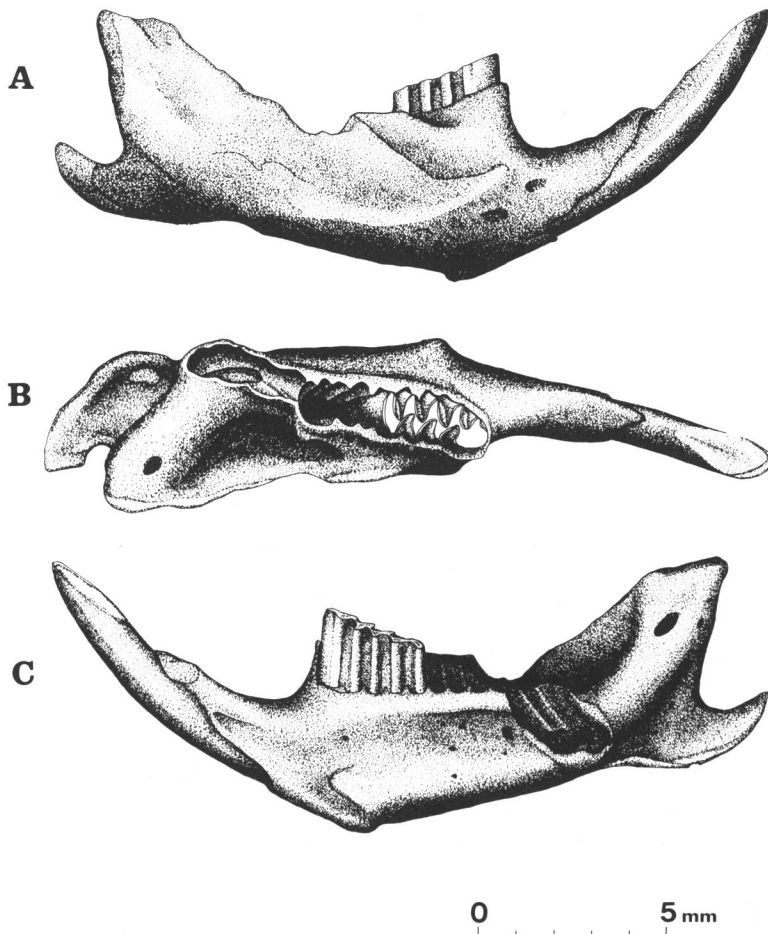


Fig. 156. Right mandible with I and M₁ of *Microtus* cf. *brandtioides* from Layer 4 of Locality 3 of Ube Kosan Quarry (KUJC96055).

A, buccal view; B, upper view; C, lingual view.

simpler than that of *M. epiratticepoides*. LSA4 is not so distinctly projected from the main part of the posterior loop as in *M. epiratticepoides*, and is almost indistinguishable from the main part. On the lingual face of the posterior loop, LRA4 is absent or merely vestigial. Consequently, Ls₄, Ls₅ and Wm are not measurable. The buccal face of the posterior loop is also smoothed and BSA4 is not formed.

Mandible —

Only three specimens are available for the present description (Figs. 156, 157). The general characters agree with the generic characters of *Microtus* already described. The position of the mandibular foramen which is preserved in one specimen only (KUJC96055) is “*agrestis* type” of HALL and YALDEN (1978).

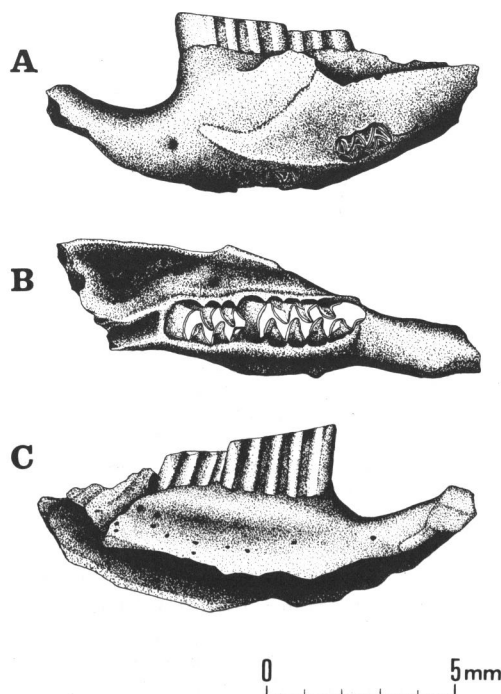


Fig. 157. Left fragmental mandible with M_1 and M_2 of *Microtus* cf. *brandtioides* from Layer 4 of Locality 3 of Ube Kosan Quarry (KUJC 97153).

A, buccal view; B, upper view; C, lingual view.

M_1 —

The molar pattern is similar to that of *M. fortis*. Is 1 to Is 6 are always closed (isthmus index less than 2.0), so that five closed triangles are formed between the anterior and posterior loops. The anterior loop is relatively broad and short.

Five salient and five re-entrant angles are observed on the lingual side. The most anterior re-entrant angle (LRA5) is poorly developed and much shallower than other re-entrant angles. The most anterior salient angle (LSA5) is generally well developed. In a few extreme variants (4, 8 and 9 of Fig. 158), however, it is rather poorly developed so that LRA5 becomes vestigial. LRA4 deeply intrudes into the anterior loop. The bottoms of LRA4 and BRA3 are somewhat alternate in position.

On the buccal side, there are three or four salient angles, and three re-entrant angles (rarely four). If present, the most anterior salient angle (BSA4) is indistinct in comparison with other salient angles. In case it is absent, the buccal wall of the anterior loop is smoothed (6, 11 and 13 of Fig. 158). In a few specimens, a very weak fold is present on the buccal wall of the anterior loop. It corresponds to BRA4 (1 and 8 of Fig. 158).

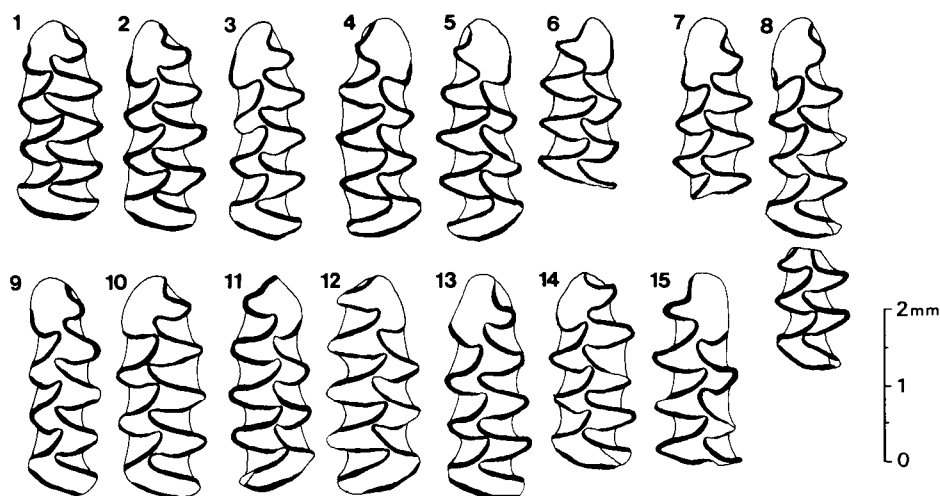


Fig. 158. *Microtus* cf. *brandtioides*. Left isolated M_1 (1–3, 7, 9, 10, 13, 14), right isolated M_1 (4–6, 11, 12, 15), and left M_1 and M_2 (8).

1–8, specimens from Locality 3 of Ube Kosan Quarry (1, KUJC96148 from Layer 8; 2, KUJC96152 from Layer 8; 3, KUJC97154 from Layer 9; 4, KUJC96055 from Layer 4; 5, KUJC96153 from Layer 8; 6, KUJC96121 from Layer 9; 7, KUJC97155 from Layer 8; 8, KUJC97153 from Layer 4); 9–12, KUJC100186 to 100189 respectively from Sugi-ana Cave; 13, unnumbered specimen from Site 5 of Yage Quarry (MATSUHASHI Collection); 14, HUA-K03780 from Horizon P of Kannondo Cave Site; 15, HUA-K03785 from the lower part of Horizon M of the same site.

M_2 —

The pattern of M_2 shares the character with those of the other species of the Japanese *Microtus*. This character is briefly described in p. 274.

Measurements

The measurements of the mandibles and molars are shown in Tables 76–78.

Comparisons

The present Japanese fossils are characterized by M_1 with five closed triangles and without BRA4 and BSA4 (even if present, they are indistinct). Among the living species of the Eurasian *Microtus*, these characters are constantly observed in M_1 of only three species such as *M. brandtii*, *M. mandarinus* and *M. fortis*.

M_1 of *M. brandtii* is similar to that of *M. mandarinus*. Both of them usually have a very simple anterior loop which is small and squarish in shape. Such an anterior loop is somewhat simpler than that of the present fossils. Furthermore, LSA5 and LRA5 are absent or only slightly developed in these two species, whereas they are rather distinctly developed in the present fossils. On the other hand, the absence or indistinctness of BSA4 and BRA4 are observed in both of them.

In *M. fortis*, the anterior loop of M_1 is more complicate than those of *M. brandtii* and *M.*

Table 76. Measurements of the mandibles of *Microtus* cf. *brandtioides* in mm. The numbers on the left side correspond to those in Fig. 72.

	Kumaishi- Loc. 3 of Ube do Cave Kosan Quarry		
	F ₃ YKS 04005	Layer 4	
		KUJC 96055	KWJC 97153
1. Total length of the mandible (id to goc)	—	16.16±	—
4. Length of the horizontal ramus	—	10.49±	—
5. Length of the diastema	—	4.09±	3.87
7. Length of the ascending ramus (the posterior border of M ₃ to goc)	—	5.86±	—
12. Maximum height of the horizontal ramus	—	3.71	—
13. Height of the horizontal ramus behind M ₃	—	2.23±	—
14. Maximum thickness of the horizontal ramus	2.81	3.16	—
16. Length of the molar row (M ₁ to M ₃) at the crowns	—	6.29±	—
17. Length of the molar row (M ₁ to M ₂) at the alveoli	—	—	4.48±
18. Ditto at the alveoli	—	4.79	4.83

mandarinus. Namely, LSA5 is well-developed, and LRA5 is mostly present. On the other hand, BSA4 is absent or inconspicuous, and BRA4 is always lacking. Therefore, except its larger size, M₁ of *M. fortis* resembles that of the present fossils in general occlusal pattern.

In regard to the morphology of the mandible, TOKUDA (1939, 1941b) noted that the depression between the alveoli of molars and the ascending ramus was inconspicuous in *M. brandtii* like *Clethrionomys*. However such a depression is distinct in *M. mandarinus* and *M. fortis*. As far as this character is concerned, the present fossils approach the last two species rather than *M. brandtii*.

M³ of *M. brandtii* and *M. mandarinus* are characterized by the anterior loop followed by three triangles and a very simple posterior loop. Only three salient angles are observed on both lingual and buccal sides. LRA4 is mostly absent. Even if present, it is very faint. M³ of the present fossils has the similar pattern to those of these species.

M³ of *M. fortis* is considerably different from those of *M. brandtii* and *M. mandarinus* in having a more complicate posterior loop which is mostly C-shaped. Such a posterior loop is most similar to that of *M. montebelli* in the fossil populations of the Japanese *Microtus*, but clearly distinct from that of the present fossils.

The above-mentioned comparisons with the three living species are summarized as follows: The M₁ pattern of the present fossils is somewhat different from those of *M. brandtii* and *M. mandarinus*, although the M³ pattern is similar. On the other hand, *M. fortis* is similar to the

Table 77. Measurements of M^3 of *Microtus* cf. *brandtioides* in mm.

LOCALITY AND SPECIMEN NUMBER	LENGTH	WIDTH
LATE PLEISTOCENE		
Kumaishi-do Cave (F_1 , F_2 and F_4)		
YKS 00277	1.70	0.86
YKS 03013	1.59	0.67
Kannondo Cave Site; Horizon 0 (upper)		
HUA-K03782	1.86	1.01
HUA-K03783	1.95	1.02
Kannondo Cave Site; Horizon 0 (lower)		
HUA-K03781	1.93	0.95
Sugi-ana Cave		
KUJC100185	1.76	0.82
MIDDLE PLEISTOCENE		
Locality 3 of Ube Kosan Quarry		
KUJC96082 from Layer 18	1.71	0.86
KUJC96106 from Layer 10	1.99	0.94
KUJC96107 from Layer 10	1.89	0.93
KUJC96158 from Layer 8	1.86	0.98
KUJC96160 from Layer 8	1.81	0.96
KUJC96161 from Layer 8	1.69	1.05
KUJC96265 from Layer 6	1.82	0.88
KUJC96018 from Layer 1	1.86	0.89
KUJC96025 from Layer 1	1.86	1.01

present fossils in M_1 pattern, but considerably different in M^3 pattern and size. Therefore none of these living species are well coincident with the present fossils, as far as the characters of the molars and mandible are concerned.

Within the Chinese fossil species of *Microtus*, *M. epiratticeps* and *M. complicidens* are easily distinguishable from the present Japanese fossils by the number of closed triangles in M_1 . *M. brandtioides* exclusively agree with the present fossils in this character. According to YOUNG (1934), this species is distinct from the closely allied *M. brandtii* by the variability of the teeth (especially M_1).

In regard to the variation of the anterior loop of M_1 , YOUNG stated that in the simplest type, the anterior loop is oval or slightly concave lingually. This type corresponds to the typical patterns of *M. brandtii* and *M. mandarinus*, but is not found in the present fossils. Another type with more or less developed LRA5 is also described and illustrated by YOUNG (22, 23 etc. of his Fig. 40). This type is similar to the majority of the present fossils. He noticed

Table 78. Measurements of M_1 and M_2 of *Microtus cf. brandtioides* in mm.
 * MATSUHASHI Collection.

LOCALITY AND SPECIMEN NUMBER	LENGTH	WIDTH
M_1		
LATE PLEISTOCENE		
Kumaishi-do Cave (F ₃)		
YKS 04005	3.03	1.24
Kannondo Cave Site; Horizon M (lower)		
HUA-K03786	2.95	1.24
HUA-K03785	—	1.18
Kannondo Cave Site; Horizon N		
HUA-K03784	2.73	1.06
Kannondo Cave Site; Horizon P		
HUA-K03780	2.60	1.14
Yage Quarry; Site 5		
Unnumbered specimen*	2.98	1.21
Sugi-ana Cave		
KUJC100186	2.89	0.99
KUJC100187	2.90	1.19
KUJC100189	2.91	1.17
KUJC100188	2.86	1.11
MIDDLE PLEISTOCENE		
Locality 3 of Ube Kosan Quarry		
KUJC97154 from Layer 9	2.82	1.03
KUJC96148 from Layer 8	2.65	1.13
KUJC96152 from Layer 8	2.78	1.11
KUJC96153 from Layer 8	2.94	1.14
KUJC96055 from Layer 4	2.88	1.10
KUJC97152 from Layer 4	2.84	1.43
KUJC97153 from Layer 4	2.89	1.09
KUJC96048 from Layer 3	2.83	1.14
KUJC97151 from Layer 3	—	1.05
M_2		
MIDDLE PLEISTOCENE		
Locality 3 of Ube Kosan Quarry		
KUJC97153 from Layer 4.	1.61	0.99

the tendency to form an outer accessory fold (BRA4) in some specimens. Such a tendency is also observable in a few specimens of the present fossils. Additionally he described that the posterior loop of M_1 is set obliquely to the axis of the tooth row in *M. brandtioides*. This character is also found in the present fossils.

M^3 of *M. brandtioides* has the very simple posterior loop which is usually confluent with T4. Its general pattern is rather similar to the present fossils, although the posterior loop of *M. brandtioides* is still simpler and the confluence with T4 is inconspicuous in the present fossils.

From these observations, it is concluded that the present fossils are most similar to *M. brandtioides* among the living and fossil species of the Eurasian *Microtus*. However some minor differences are also observed between them; namely the absence of the simplest type of M_1 in the present fossils (this type is considerably abundant in the assemblage of *M. brandtioides*); and more complicate posterior loop of M^3 in the present fossils. Therefore the present fossils are tentatively assigned to *M. cf. brandtioides* here. Because the materials are now insufficient, the specific allocation of this form will be settled by the further investigations based on the adequate materials obtained in future.

Discussion

KOWALSKI and HASEGAWA (1976) included the present form in their "*M. epiratticeps*" as its extreme variant. In the living population of *M. oeconomus*, in deed, M_1 with five closed triangles are rarely found, although the majority of them carries four closed triangles. But if YOUNG's classification for the Choukoutien materials (1934) is applied to the Japanese materials as done by KOWALSKI and HASEGAWA, M_1 with five closed triangles and with a relatively simple anterior loop should be identified as *M. brandtioides*. It is very difficult to decide whether this form is an independent species or the extreme variant of *M. epiratticepoides*.

In the preceding sections, the present author treated this form as a separate species from *M. montebelli* and *M. epiratticepoides* by the reason that it is easily distinguishable from these two species by its M_1 and M^3 patterns and the intermediate forms among them are considerably scarce. In order to confirm the validity of such a treatment, the relationship among M_1 patterns of these three forms are examined here.

As already mentioned, M_1 of these three forms can be separated by the isthmus index and the degree of the development of BSA4 or BRA4. Moreover these criteria provide the distinction among the morphotypes of *M. epiratticepoides*. The relationship among the three forms including the morphotypes of *M. epiratticepoides* is given in Fig. 159. As regards the criteria, M_1 of *M. montebelli* and the present form are rather uniform in morphology, while that of *M. epiratticepoides* is quite variable so that six morphotypes are recognized. The morphotype Iu of *M. epiratticepoides* is regarded as the intermediate type between the present form and one of the typical patterns of *M. epiratticepoides* (Ou), although it is nearer to the latter. The same circumstances are observed in the morphotype Id which is the intermediate type between *M. montebelli* and another typical pattern of *M. epiratticepoides* (Od).

In the Middle Pleistocene locality (Locality 3 of Ube Kosan Quarry), the occurrences of Iu and Id are somewhat fewer than those of *M. montebelli* and the present form (Fig. 159). In the

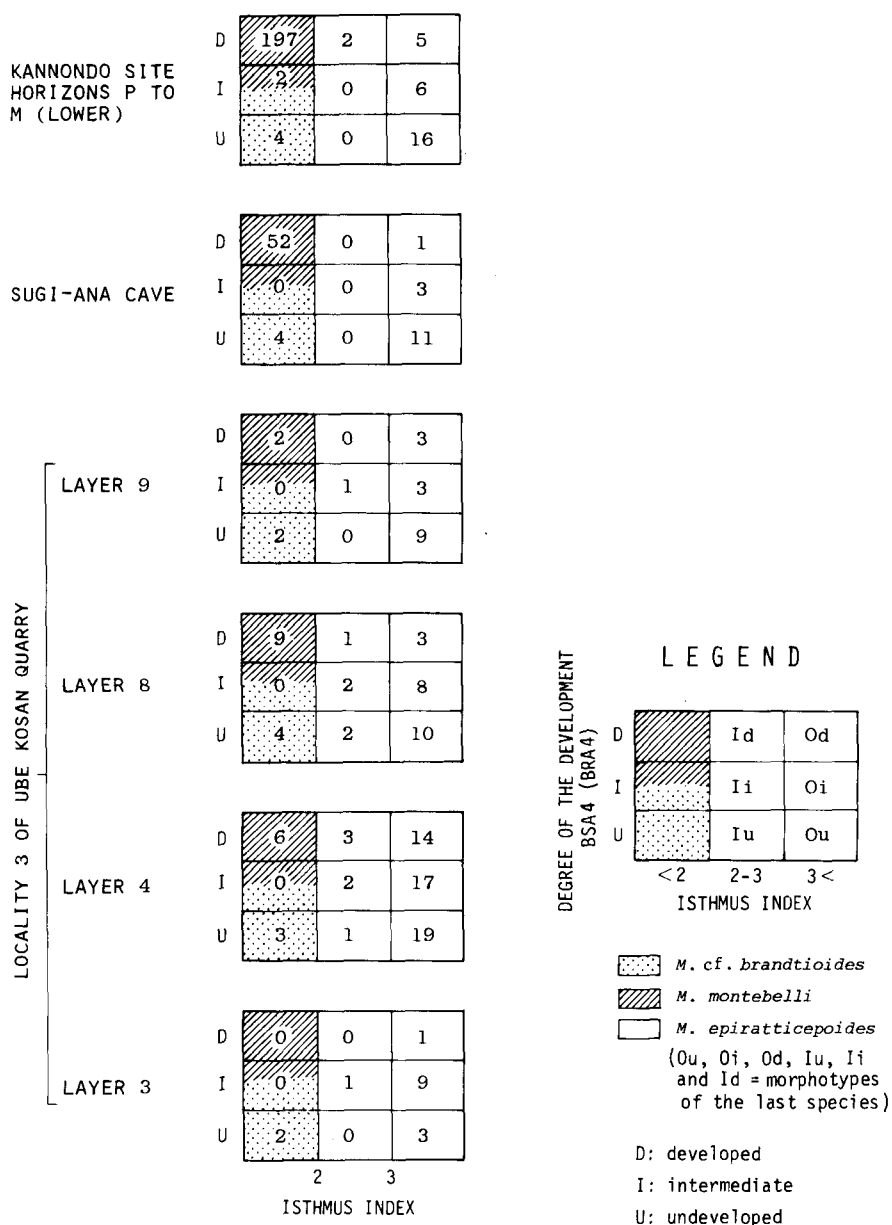


Fig. 159. Morphological interrelation among M_1 of the three forms of the Japanese *Microtus*. In accordance with the isthmus index and the degree of the development of BSA4 (BRA4), the examined specimens are classified into nine types (including the six morphotypes of *M. epiratticepoides*). The number of the specimens belonging to each type is given. For example, in the examined specimens of Sugi-ana Cave (71 specimens), 11 specimens belong to the morphotype Ou (isthmus index more than 3, and BSA4 undeveloped), which is shown in the right-lower domain.

Late Pleistocene localities, Iu is completely absent and Id is very rare. Moreover the occurrence of the present form is not so few in some cases in comparison with that of *M. epiratticepoides* (for example, Horizons M, N and P of Kannondo Cave Site in Fig. 67), although both of them are much fewer than that of *M. montebelli*. If the present form is the extreme variant of *M. epiratticepoides*, it is absent or very rare in such localities where *M. epiratticepoides* is few in number.

Judging from these facts, it is most probable that the present form belongs to an independent species from *M. epiratticepoides* and *M. montebelli*.

This form seems to be closely related to the Chinese *M. brandtioides* which is abundantly known from the Middle and Late Pleistocene localities of North China. It possibly migrated from North China into Japan in the early Middle Pleistocene accompanying *M. epiratticepoides*. In contrast with *M. epiratticepoides*, this form had been left as a minor element within the Japanese *Microtus* populations, until it was extinguished in the Latest Pleistocene. The time of the extinction is estimated to be 10,000 to 15,000 yr. B.P., which is contemporaneous with that of *M. epiratticepoides*.

(to be continued to Part 2)