Quaternary Mammalian Faunas in the Japanese Islands¹⁾

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The faunal succession of Japanese Quaternary mammals is described within the stratigraphic framework provided mainly by KAMEI, KAWAMURA and TARUNO (1988). Descriptions are given separately for Hokkaido, Honshu—Shikoku—Kyushu and the Ryukyu Islands.

In Hokkaido, Pleistocene mammalian remains are too scarce to provide a detailed faunal succession, but abundant remains of Holocene age suggest that the fauna was almost identical to that of the present day. Large mammals recorded for the Late Pleistocene are therefore considered to have been extinct by the Holocene.

In Honshu—Shikoku—Kyushu, the Early Pleistocene fauna is of temperate forest type, and related to those of north China. Almost all the components are, however, assigned to extinct endemic species. The Middle Pleistocene fauna is characterized by the presence of extant species. In fact, they exceed half of the components in the middle Middle Pleistocene fauna, and are still more common in the later faunas. This fauna is also dominated by temperate forest elements and endemic species. Immigration from south China in the middle Middle Pleistocene is more limited than previously thought, and only a few forms migrated from north and northeast China in the late Middle Pleistocene. The Late Pleistocene fauna is basically identical with that of the Middle Pleistocene except for the absence of several extinct species and several exotic species which still survive in other regions. Although the fauna seems to have been isolated from those of the adjacent continent in the early Late Pleistocene, immigration of large herbivores from the northern part of the continent was recognized in the late Late Pleistocene. Most of the extinct and exotic species were eliminated from the fauna between 20,000 and 10,000 years BP, and thus the fauna became almost identical with that of the present day by the early Holocene.

In the Ryukyu Islands, Early and Middle Pleistocene faunas are almost unknown, while Late Pleistocene and Holocene ones are relatively well recorded. The Late Pleistocene fauna is of insular type, and includes several species endemic to the islands. Some of them are extinct species. From the end of the Pleistocene to the Holocene, insularity of the fauna was enhanced by the extinction of major species and by extreme reduction in habitat areas of the survivors.

I. Introduction

In the Japanese Islands, Quaternary mammalian remains are occasionally found in fluvio-lacustrine and marine sediments, and in cave and fissure sediments. They are also dredged from the bottom of shallow seas. One of these finds was first reported in scientific literature about 120 years ago (ADAMS, 1868). Since then, they have been studied by a number of paleontologists, and several important contributions have been made to their taxonomy, geologic

age and relationship with continental species. However, it was rather recent that the faunal succession of the mammals was fully understood within a precise stratigraphic framework. KAMEI and SETOGUCHI (1970), and KAMEI and OTSUKA (1981) studied the stratigraphic distribution of proboscidean remains in representative fluvio-lacustrine and marine sediments which were carefully investigated by stratigraphic, chronological and paleobotanical methods, and proposed a mammalian biozonation of the sediments. In addition, KAWAMURA

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(1988) gave a comprehensive account of the stratigraphic relationships of fossiliferous cave and fissure sediments in his monograph on Quaternary rodents of Japan. On the basis of these works as well as the results of other recent studies, KAMEI, KAWAMURA and TARUNO (1988) improved the above-mentioned biozonation and proposed newly designated zones, such as QM 1 to QM 8 (see Fig. 2), and described the faunal contents of each zone.

This paper presents a brief review of the Quaternary mammalian faunal succession, which is based mainly on the stratigraphic framework of KAMEI, KAWAMURA and TARUNO (1988), but also includes more recent data and interpretation of the fauna (partly given in KAWAMURA *et al.*, 1989).

II. Biogeographic regions

The Japanese Islands can be divided into the three biogeographic regions of Hokkaido, Honshu-Shikoku-Kyushu and the Ryukyu Islands based on the present-day distribution of terrestrial mammals. The fauna of the first region is mostly similar in species to that of the adjacent continent, while the fauna of the second region is dominated by endemic species. In the third region, the fauna is of insular type, and includes highly endemic forms. These differences are attributable to differences in the Quaternary geohistory of each region. Therefore, in the following chapters, the Quaternary mammalian faunas and their succession are described separately for each region.

III. Hokkaido

Mammalian remains hitherto recorded are too scarce or too biased chronologically to allow discussion of detailed faunal succession. In particular, records of Early Pleistocene mammals are almost unknown. Middle Pleistocene mammals are, however, rarely found in fluvio-lacustrine and marine sediments in the Ishikari Lowland (Figs. 1, 2). They are represented by archaic mammoths (*Mammuthus* cf. *paramamonteus* and *M.* cf. *armeniacus*), a bison (*Bison* sp.) and marine mammals (*Odobenus* sp. and *Hydrodamalis gigas*) (KIMURA *et al.*, 1983 etc.). Because the mammoths are also found in the

Middle Pleistocene of Honshu, the faunas of both areas were probably related, at least some time in the Middle Pleistocene.

Late Pleistocene mammals are rarely recovered from fluvial and marine terrace deposits, and from neritic sea bottoms. Taxa recorded are represented by only two species of elephant, *Palaeoloxodon naumanni* and *Mammuthus primigenius*. The former occurs abundantly in the Late Pleistocene of Honshu-Shikoku-Kyushu, but the latter has never been found there. Notwithstanding the presence of the common element, the faunal exchange between Hokkaido and Honshu-Shikoku-Kyushu is considered to have been greatly restricted in the Late Pleistocene (KAWAMURA, 1985; KAWAMURA *et al.*, 1989).

Remains of Holocene age are abundant in archaeological sites. They indicate that the fauna was almost identical to that of the present day except for a few alien forms which were possibly introduced by man. The elephants of the Late Pleistocene are never found in the Holocene fauna, and hence they probably became extinct before the Holocene.

IV. Honshu-Shikoku-Kyushu

1. Early Pleistocene

Mammalian remains are rarely found in Early Pleistocene fluvio-lacustrine and marine sediments in central Honshu and west Kyushu, including the Kazusa, Uonuma, Age, Kobiwako, Osaka and Kuchinotsu Groups (Fig. 2). The members of the fauna are restricted to elephants, artiodactyls and marine mammals, which are all extinct at the specific level or even the generic level. They include *Stegodon aurorae* (= *S. akashiensis* and *S. sugiyamai*), *Mammuthus* spp., *Elaphurus shikamai*, *E. akashiensis*, *Cervus* (*Rusa*) *kyushuensis*, *C. (Axis) japonicus*, *C. (Nipponicervus) kazusensis*, *Pseudorca yokoyamai* and *Oriensarctos watasei*. Of these, the terrestrial mammal fauna is of temperate forest type. Until recently, the fauna had been believed to possess a mixture of the Siva-Malayan and Nihowan faunas. Recent studies, however, suggest that *Stegodon aurorae* once considered as a typical Siva-Malayan element is closely related to elephants of north China, and hence the fauna is

Fig. 1 Location map of the principal Quaternary mammalian fossil localities in Japan

Dotted area : Localities on the sea bottom (1. Nemuro Strait, 2. Seto Inland Sea, 3. Japan Sea off San-in, 4. Ariake Bay)

almost completely composed of elements related to those of north China (KAMEI, TARUNO and KAWAMURA, 1988 ; SAEGUSA, 1990). At the specific level, however, the recorded taxa are mostly endemic. This indicates that the fauna was already isolated from that of the adjacent continent.

From the biostratigraphic viewpoint, the Early Pleistocene can be divided into two parts, QM 1 and QM 2 (Fig. 2). QM 2 is characterized by the appearance of the primitive mammoth,

Mammuthus paramammonteus shigensis, which is absent from QM 1. The first appearance of this form around 1.0 Ma probably indicate a remarkable immigration of the mammoth group from the northern part of the continent, although a possible occurrence of *Mammuthus* in the Uonuma Group is assigned to QM 1 (Fig. 2).

2. Middle Pleistocene

Early Middle Pleistocene (QM 3)

As pointed out by KAWAMURA and IIDA (1989), mammalian remains are little known from the

early Middle Pleistocene, and the bulk of our knowledge on the fauna comes from sparse remains obtained from lacustrine sediments in the upper part of the Kobiwako Group (Fig. 2). They include mouse (*Apodemus argenteus*), elephants (*Stegodon aurorae* and *Mammuthus paramammonteus shigensis*), deer (*Cervus kazusensis*) and a water buffalo (*Bubalus* sp.). Most of them are extinct species. KAWAMURA *et al.* (1989) considered, on the basis of such evidence, that the fauna was transitional between the Early Pleistocene fauna and the typical Middle Pleistocene one.

Middle Middle Pleistocene (QM 4)

Mammalian remains are much more abundant than in the preceding periods (QM 1 to QM 3). They are found in fluvio-lacustrine and marine sediments (e.g. upper parts of the Kazusa and Osaka Groups), and in cave and fissure sediments (e.g. Lower Kuzutō Formation and Ikumo Quarry). Remains dredged from the bottom of the Seto Inland Sea (Fig. 1) are partly assignable to this period, although most of them are probably younger (QM 5 to QM 7).

The fauna includes a hedgehog (*Erinaceus* sp.), extinct shrews (*Anourosorex japonicus* and *Shikamainosorex densicungulata*), extant shrews (*Sorex shinto* and *Crociodura dsinezumi*), shrew-moles (*Dymecodon pilirostris* and *Urotrichus talpoides*), moles (*Euroscaptor mizura* and *Mogera wogura*), extinct bats (*Pleistomyotis longihumeralis*, *Myotis okafujii* and *M. beppuensis*), a hamster (*Cricetulus* sp.), wood lemming (*Myopus schisticolor*), extinct voles (*Clethrionomys japonicus*, *Microtus epiratticepoides* and *M. cf. brandtioides*), mice (*Apodemus speciosus* and *A. argenteus*), dormouse (*Glirulus japonicus*), extinct killer whale (*Orcinus paleorca*), wolf (*Canis lupus*), racoon dog (*Nyctereutes procyonoides*), fox (*Vulpes vulpes*), extant weasel (*Mustela sibirica*), extinct weasel (*M. constricta*), extinct badgers (*Meles leucurus kuzuensis* and *M. mukasianakuma*), extinct walrus (*Odobenus mandanoensis*), extinct elephants (*Stegodon orientalis* and *Mammuthus* spp.), extinct rhinoceros (*Rhinoceros sinensis*), extinct wild boar (*Sus* cf. *lydekkeri*), musk deer (*Moschus moschiferus*), extinct giant deer (*Sinomegaceros yabei*) and extinct deer (*Cervus praenipponicus* and *C. kazusensis*).

About half of the taxa recorded is assigned to extinct species, and exotic species which are absent from this region at the present day, and the remainder is extant. On the other hand, the fauna is dominated by temperate forest elements, but includes a few immigrants from south China, namely warm temperate forest elements of the Wanhhsien fauna (e.g. *Stegodon orientalis* and *Rhinoceros sinensis*). Previous students overemphasized the presence of these immigrants and advocated a major immigration from south China, because information about the fauna was inadequate and biased toward large mammals. The above-mentioned more complete faunal list and close comparison with Chinese faunas suggest that the immigration is not as remarkable as previously considered (KAWAMURA *et al.*, 1989). However, the first appearance of the most representative immigrant, *Stegodon orientalis*, is important from a biostratigraphic viewpoint, and is dated to around 0.5 Ma (Fig. 2 ; cf. KAMEI, KAWAMURA and TARUNO, 1988).

The fauna is also characterized by a high percentage of endemic species (more than 50 %). These species are considered to have achieved their evolutionary status as indigenous by the middle Middle Pleistocene, and more than half of them have survived until the present day.

Late Middle Pleistocene (QM 5)

The information on the fauna of this period is obtained mainly from cave and fissure sediments (e.g. Localities 1 and 3 of Ube Kosan Quarry). In addition, marine and fluvio-lacustrine sediments (e.g. lower part of the Shimosa Group) yield sparse material from marine and large terrestrial mammals (Fig. 2).

The fauna of this period is similar to that of the middle Middle Pleistocene, but lacks the hedgehog, extinct bats, wood lemming, hamster, extinct elephants, and extinct rhinoceros which occur in the latter fauna. On the other hand, only a few forms are newly added to the fauna. They include extant vole (*Microtus montebelli*) and extinct elephant (*Palaeoloxodon naumanni*), which probably immigrated from northeast and north china. The first appearance of the elephant is estimated to be around 0.3 Ma (Fig. 2), whereas that of the vole is somewhat later.

The fauna of this period is clearly of temperate forest type with predominantly endemic species. Its character has remained unchanged until the present day. The percentage of extant species is somewhat higher than that of the preceding period.

3. Late Pleistocene

Early Late Pleistocene (QM 6)

Mammalian remains are found in cave and fissure sediments (e.g. Shiriya Quarry, Upper Kuzuü Formation, Sugi-ana Cave and Locality 2 of Ube Kosan Quarry), and marine and fluvio-lacustrine sediments (e.g. upper part of the Shimosa Group, and the Nishiyagi Formation). The fauna is basically equivalent to that of the late Middle Pleistocene, but is slightly different in the presence of the vole (*Clethrionomys-Phaulomys* transitional form) which is a descendant of the Middle Pleistocene vole, *Clethrionomys japonicus*, and in the relatively low occurrence of the extinct small mammals, *Anourosorex japonicus* and *Microtus epiratticepoides*. The fauna of this period seems to contain no newly added immigrants, and hence the fauna is probably isolated from those of the adjacent continent (KAWAMURA *et al.*, 1989).

Late Late Pleistocene (QM 7)

The fauna of this period is better known and dated than that of the early Late Pleistocene. It is represented by local faunas from the cave and fissure sediments of Kumaishido Cave and Kannondo Cave Site, and from the fluvial Hanaizumi Bed and lacustrine Nojiri-ko Formation. The fauna generally resembles that of the preceding period, but lacks several extinct and exotic forms including *Shikamainosorex densicingulata*, *Mustela kuzuensis*, *Meles leucurus kuzuensis*, *Martes ten* (extinct marten) and *Moschus moschiferus*. Furthermore, it contains a few forms of large herbivores which newly immigrated from the northern part of the continent. They include a horse (*Equus* sp., *E. hemionus* or *E. nipponicus*), elk (*Alces alces*), aurochs (*Bos primigenius*) and extinct bison (*Bison priscus*), but neither woolly mammoth (*Mammuthus primigenius*) nor woolly rhinoceros (*Coelodonta antiquitatis*). Because Hokkaido is considered to have been connected by land to the continent through the interposition of Sakhalin

in this period, KAWAMURA (1985, 1989) postulated ice bridges between Honshu and Hokkaido through which the immigrants had migrated.

The survivors of the extinct and exotic species (e.g. *Microtus epiratticepoides*, *Palaeoloxodon naumanni* and *Sinomegaceros yabei*) as well as the above-mentioned immigrants were mostly eliminated from the fauna between 20,000 and 10,000 years BP, and no mammals larger than Sika deer (*Cervus nippon*), wild boar (*Sus scrofa*) or black bear (*Selenarctos thibetanus*) survived later than 10,000 years BP. This extinction phenomenon seems to have been caused at least partly by human hunting activities, and it possibly had an impact on the life of early man. The phenomenon is therefore considered to be strongly related to the cultural transition from the Paleolithic to Jomon around 12,000 years BP.

4. Holocene

Mammalian remains are abundant in a number of archaeological sites of this period. They indicate that the fauna is identical to that of the present day except for the rare occurrence of exotic species, including lynx (*Lynx lynx*). The fauna of this period is characterized by the predominance of Sika deer and wild boar, which were the most important game for Jomon hunters. In the Late Pleistocene fauna, the former and its relatives commonly occur in association with other extinct deer, while the latter is very rare. As pointed out by KAWAMURA (1981) and KAWAMURA *et al.* (1990), the wild boar greatly increased in number at the beginning of the Holocene.

V. The Ryukyu Islands

Early and Middle Pleistocene mammalian remains are too scarce to reconstruct any faunal succession. On the other hand, Late Pleistocene ones are relatively abundant, and most of them are obtained from cave and fissure sediments (e.g., Minatogawa Site; Fig. 2).

The Late Pleistocene fauna is of insular type, because it is low in variety and lacks large mammals. Moreover, the fauna is dominated by endemic species, which belong to partly endemic genera. In the central part of the islands including Okinawa Island (Fig. 1), the fauna is, in particular, highly endemic, and

includes spiny rats (*Tokudaia osimensis* and *Diplothrix legata*), wild boar (*Sus leucomystax taiwanus*), extinct muntjacs (possibly new species of a new genus), and extinct deer (*Cervus astylodon*) (HASEGAWA, 1980; KAWAMURA, 1988 etc.). Some of these possibly originated from pre-Pleistocene ancestors. On the other hand, the fauna of the southern part including Miyako Island (Fig. 1) is considerably different. Namely, it includes voles (*Microtus oeconomus*, *M. fortis* and *M. sp.*), *Diplothrix legata*, a cat (*Felis sp.*), wild boar (*Sus scrofa*), extinct roe deer (*Capreolus miyakoensis*) and *Cervus astylodon* (HASEGAWA, 1985 etc.). Some of them show similarities to the Palaearctic fauna.

Remains of Holocene age are obtained mainly from archaeological sites. The fauna is still less variable compared to that of the Late Pleistocene. It includes the spiny rats (both of the species) and the wild boar (possibly *Sus scrofa*), but generally lacks the muntjacs, roe deer and deer. During the Holocene, even the spiny rats and wild boar became extinct on a number of islands, and thus their present-day distribution is extremely restricted.

VI. Conclusion

In Hokkaido and the Ryukyu Islands, the faunal succession is insufficiently understood, because information for Early and Middle Pleistocene mammals is extremely scarce. In Honshu-Shikoku-Kyushu, however, mammalian remains are more abundant. They indicate that the fauna of this region has been of temperate forest type with predominantly endemic species throughout the Pleistocene. This is possibly attributable to the predominance of temperate forest environments and periodical isolation of long duration from continental faunas. Although immigration from the adjacent continent is sometimes recognized, it is not as remarkable as previously considered. The fauna has changed gradually in comparison with conditions in Europe where drastic faunal changes were detected in association with glacial-interglacial cycles (especially since the Middle Pleistocene). This possibly results in milder climatic and vegetational changes in this region during the

Pleistocene. The last remarkable mammalian extinction took place between 20,000 and 10,000 years BP, and thereby large mammals were eliminated from the fauna. This phenomenon seems to have been closely related to the cultural transition from the Paleolithic to Jomon. The remaining mammals constituted the Holocene fauna, which is characterized by high proportions of endemic and sylvan forms, and by the presence of several relict forms.

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