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First Discovery of Fossil Amami Rabbit (*Pentalagus furnessi*) from Tokunoshima, Southwestern Japan

by

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Abstract Two upper molariform teeth (right M^1 and left P^3) of Amami rabbit, *Pentalagus furnessi* (STONE), were found from Tokunoshima as the first fossil record. Their geologic age is very likely the latest Pleistocene. Both teeth are one of the least identifiable elements among the lagomorph dental material in general, but the enamel pattern of *Pentalagus* teeth are so distinctive that it is possible to identify them as *P. furnessi*. They occurred with the extinct deer *Cervus astylodon*, suggesting that Amami rabbit might have arrived at about the same time period and through the same migration route as *C. astylodon* during the early Middle Pleistocene.

Introduction

Amami rabbit, *Pentalagus furnessi* (STONE), is currently living only in the Amamioshima and Tokunoshima of the Amami Islands, southwestern Japan (Fig. 1). It has been well known as one of the living fossils and its isolated distribution (the closest extant relative is *Pronolagus* living in southern Africa). Fossil material of *P. furnessi* has not been known. *Pliopentalagus* GUREEF has been thought to be the ancestor of *Pentalagus* LYON (*e.g.*, DAXNER & FEJFAR, 1967; HIBBARD, 1963*), but no fossils that link these two genera have been known either, although *Pliopentalagus* has recently been known from the late Pliocene in China (CAI, 1989).

Two upper molariform teeth of *Pentalagus* were found in 1990 from the travertine that was formed to fill a fissure in the limestone of Ryukyu Group. The same sediments have produced the remains of an extinct deer, *Cervus astylodon* MATSUMOTO, that was the only vertebrate fossil known from Tokunoshima before (OTSUKA *et al.*, 1980). Discovery of these teeth and a brief abstract on their identification were presented by TOMIDA *et al.* (1990) and TOMIDA and OTSUKA (1991), respectively. The present paper is the detailed description of those fossils.

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* He placed the species "*Alilepus*" *dietrichi* as the ancestor of *Pentalagus*. The genus *Pliopentalagus* was not known at that time. "*A.*" *dietrichi* was later assigned to the genus *Pliopentalagus* by DAXNER and FEJFAR (1967).

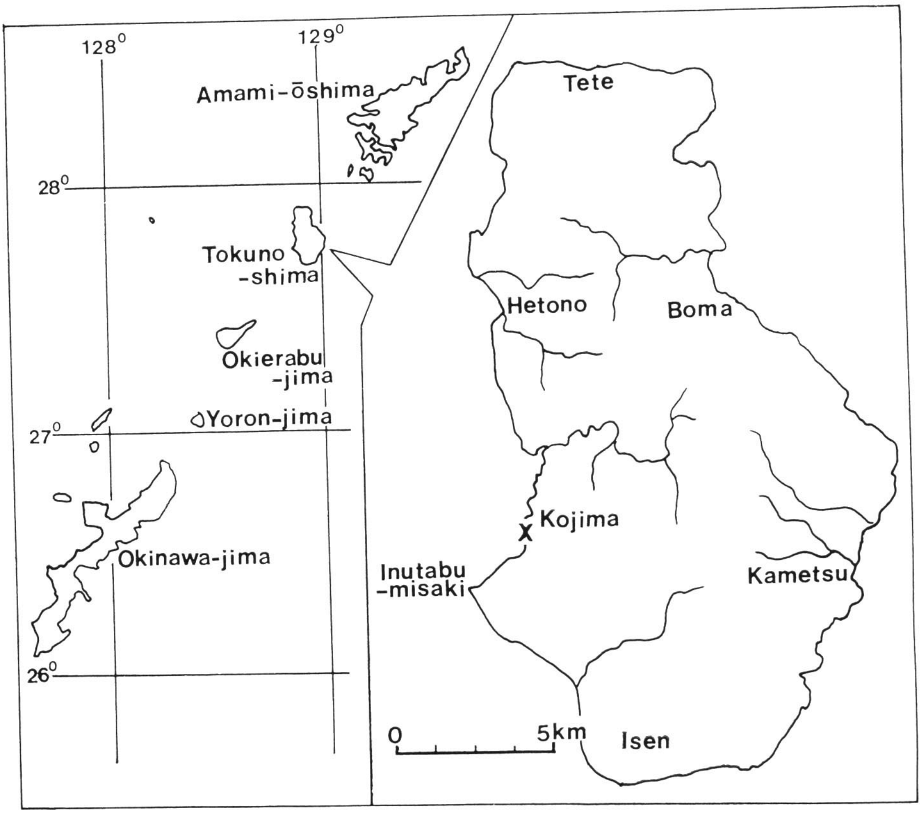

Figure 1. Map showing the locality (X mark) of fossil *Pentalagus furnessi*.

the information on the fossil-bearing travertine, and Drs. Teruya UYENO and Hisao BABA of the National Science Museum, Dr. Hajime SAKURA of Sapporo Gakuin University, Mr. Etsuhiro TOMI of Isen-cho Museum of History and Folklore, and Messrs. Yukihide MATSUMOTO, Takashi KATO, and Hajime TARU, then students of Kagoshima University for their help in the field and laboratory work. We aslo thank Prof. Hayao NISHINAKAGAWA of Kagoshima University and Mr. Hideki ENDO of the National Science Museum for allowing us to examine collections, and Drs. UYENO and Tomoki KASE of the National Science Museum for reading the manuscript and making helpful suggestions.

Locality, Occurrence, and Geologic Age

The fossil locality is situated in the middle of a sea cliff located about 700 meters west of Kojima, Isen-cho in Tokunoshima, Kagoshima Prefecture (Fig. 1). The fossil-bearing deposits are the travertine that filled a fissure formed in the Itokina

Formation of Ryukyu Group (NAKAGAWA, 1967), which is comparable to Sakibaru Formation of IRYU and YAMADA (1991). The Itokina Formation in this area consists of grayish to yellowish light brown limestone containing foraminifers and corals. The sea cliff is about 100 meters in height, and the fissure is located about 70 meters above the sea level (see OTSUKA, 1990, for detail).

The fossil-bearing travertine may have been formed nearly parallel to the cliff, and only slight amount remains there at present. This hard travertine contained a great number of deer fossils (*Cervus astylodon*) (OTSUKA, 1990). When the travertine was processed by acetic acid for obtaining deer fossils, considerable amount of remnants remained. The remnants consisted of mostly small fragments of deer bones but also contained several specimens of small vertebrates. They are: Ophidea family indet. (three vertebrae), *Pentalagus furnessi* (two upper molariform teeth), *Diplothrix legata* (eight teeth), and *Tokudaia osimensis* (two teeth). Among them, the remains of *Pentalagus furnessi* are described in this paper.

The geologic age of the fossil-bearing travertine is not certain. There is no definite evidence that indicates a specific geologic age. But, the Itokina Formation is the late Middle Pleistocene (NAKAGAWA, 1967; IRYU & YAMADA, 1991), and the cave and fissure deposits that have yielded numerous deer and other mammal fossils in Okinawa-jima, Ie-jima, and Miyako-jima are within 30,000 to 18,000 years BP (TAKAI & HASEGAWA, 1971; HAMADA, 1985; OTSUKA, 1990). Thus, the geologic age of the travertine that yielded the first Amami rabbit fossils is tentatively thought to be the Würm glacial age of the late Pleistocene, probably some 30,000 to 18,000 years BP.

Systematic Description

Order LAGOMORPHA BRANDT, 1855

Family LEPORIDAE GRAY, 1821

Subfamily LEPORINAE TROUESSART, 1880

Genus ***Pentalagus*** LYON, 1904

Pentalagus furnessi (STONE, 1900)

(Figs. 2 and 3–a, b)

Referred material: Institute of Earth Sciences, Faculty of Science, Kagoshima University (ESK)-F-6043 (right M^1) and ESK-F-6044 (left P^3) from the fissure filling travertine near Kojima, Tokunoshima (see the locality section above).
Age: Very likely the latest Pleistocene (see the geologic age section above).
Description: ESK-F-6043 is a fully developed right M^1. General morphology is typical of leporine upper molariform teeth. Antero-posterior length and maximum width are 2.1 and 3.4 mm, respectively, and preserved maximum height is 9.1 mm. The anterior loph is wider than the posterior loph, expanding anterolabially, indicative

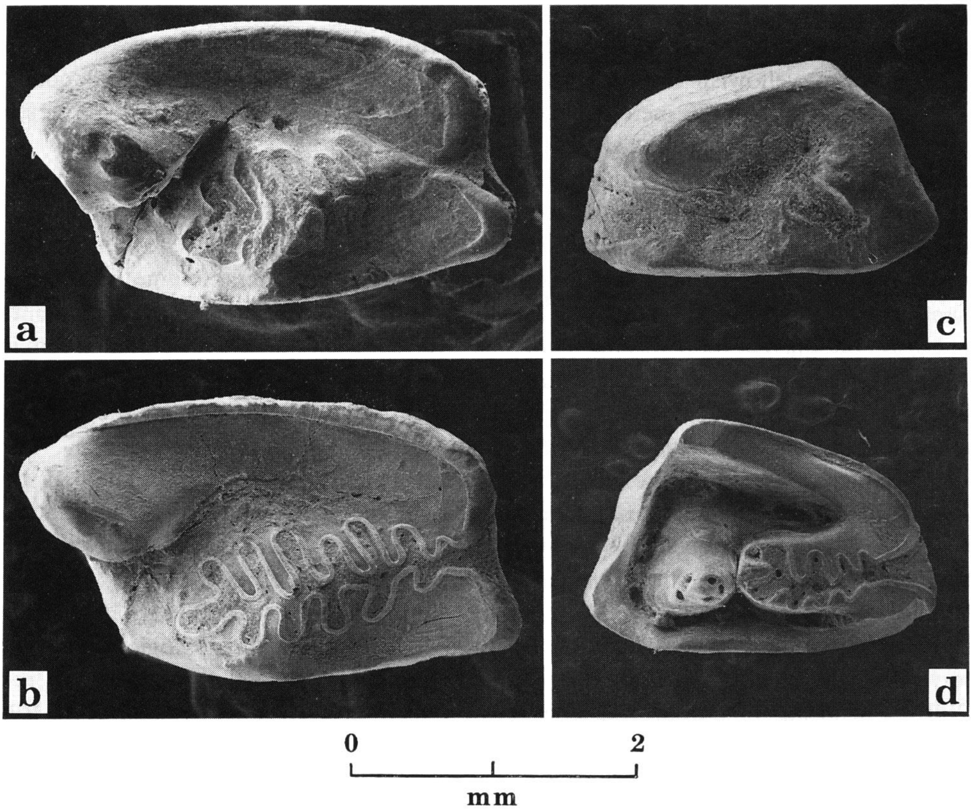

Figure 2. SEM photos of fossil *Pentalagus furnessi* from Tokunoshima.
a: ESK-F-6043, right M^1, occlusal view; b: ESK-F-6043, occlusal view after etching by hydrochloric acid; c: ESK-F-6044, left P^3, occlusal view after etching; d: ESK-F-6044, broken surface about 1.5 mm above the occlusal surface, viewing from the tooth bottom, after etching.

of M^1 or M^2. The tooth was partly broken and was missing the occlusal surface of postero-lateral corner, so that the enamel pattern of the internal reentrant fold at that part was not clear by SEM because of no difference in height among the enamel, dentine, and cementum (Fig. 2–a). Therefore, the specimen was etched by 0.5% hydrochloric acid for one minute before taking SEM photos (Fig. 2–b). The internal reentrant fold is very deep, about two thirds of the maximum width or nearly 80% of the width of posterior loph. Enamel crenulations count six (plus one small one) on anterior enamel wall, five on posterior, and one in between; each crenulation is quite deep.

ESK-F-6044 is a nearly unerupted left P^3 and is broken at the position about 1.5 mm above the occlusal surface. Development of the dentine is incomplete as evidenced by a deep hollow seen on the broken surface (Fig. 2–d). Length and width of

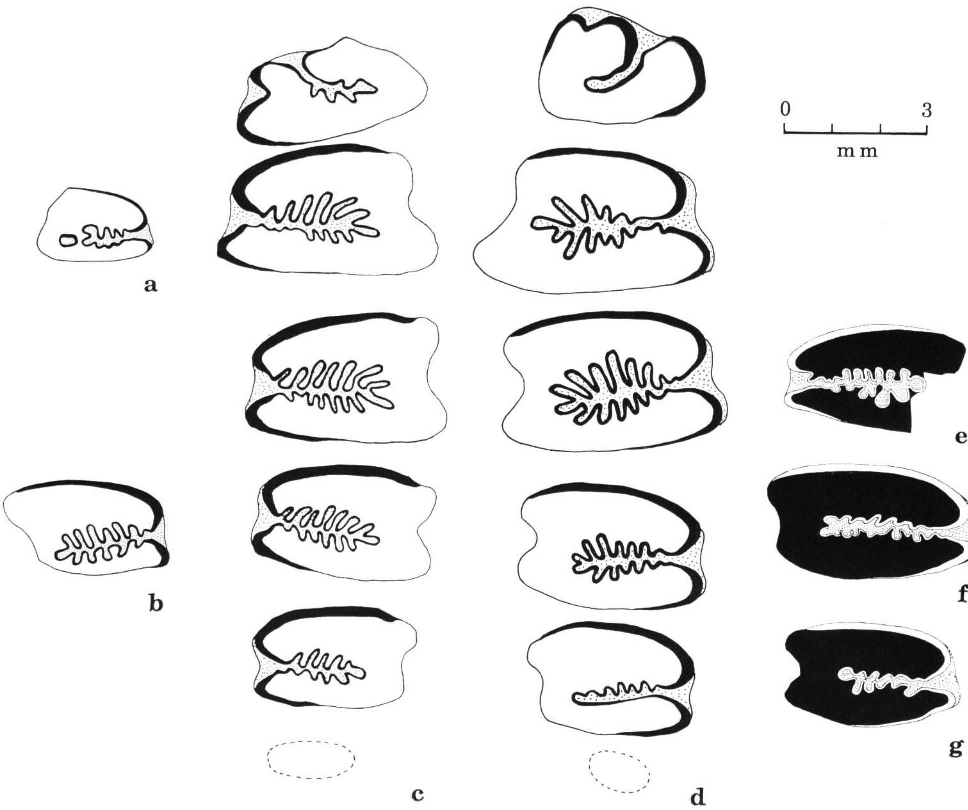

Figure 3. Upper dentitions of fossil and recent *Pentalagus* and *Pliopentalagus*.
a–b: fossil *Pentalagus furnessi*. a, ESK-F-6044, left P^3, view from the tooth bottom; b, ESK-F-6043, right M^1. c–d: recent *Pentalagus furnessi*. c, NSMT-M 12938, left P^2-M^2; d, NSM-PO 133, right P^2-M^2. e–g: *Pliopentalagus dietrichi*. e, left P^4 or M^1; f, right M^1; g, right M^1. All in occlusal view except for a. E-g from Daxner and Fejfar (1967, Abb. 3).

the tooth at the broken surface are 1.6 and 2.4 mm, respectively. Those on the occlusal surface are both considerably smaller, indicating that both measurements would be much larger if the tooth is fully grown. The anterior loph is considerably narrower than the posterior loph. The occlusal surface is covered with thin travertine layer so that the enamel pattern is nearly invisible (Fig. 2–c). The enamel pattern is fortunately visible on the broken surface, but again it is not observable by SEM. Thus, this tooth was also etched by hydrochloric acid before taking photo and sketching (Figs. 2–d and 3–a). The internal reentrant fold is fairly deep, about 60% of the tooth width. Enamel crenulations count four on both anterior and posterior enamel walls. An enamel lake is located labial to the internal reentrant fold. It is expected that they would be connected when the tooth further grows; in that case the depth of the internal reentrant fold may reach nearly three fourths of the tooth width.

Comparisons: Fairly detailed description and illustrations of the dentitions of *Pentalagus furnessi* were first given by LYON (1904). But, the following comparisons were made directly with the collections of the National Science Museum, Japan. ESK-F-6043 is identified as an M^1 based on the general morphology of the enamel pattern and the width of the anterior loph wider than the posterior loph. The possibility to be a P^4 or an M^2 is nearly negligible because of the wider anterior loph and much more complicated enamel crenulation, respectively (see Figs. 3–b, c, d). ESK-F-6044 is identified as a P^3 based on the outline of the cross section in which the anterior loph is much narrower than the posterior. The depth of the internal reentrant fold would be very deep if the presently-isolated enamel lake is connected, and this fact, together with the narrower anterior loph, eliminates the possibility to be an M^2.

The upper molariform teeth are, in general, the least identifiable elements among the lagomorph teeth. However, the enamel pattern of *Pentalagus* teeth is the most complicated one among the lagomorph genera, and the upper molariform teeth are not an exception. Thus, ESK-F-6043 and 6044 can be referred to the genus *Pentalagus* based on the complexity of the enamel crenulation. The enamel crenulation and the depth of each crenulation of the upper molariform teeth in *Pliopentalagus* are less complicated and much shallower, respectively, than those of *Pentalagus*. *Aztranolagus agilis* (RUSSELL & HARRIS, 1986) has P_3 that is superficially similar to that of *Pentalagus*. But, the enamel crenulation of the upper molariform teeth in *Aztranolagus* is much shallower than in *Pentalagus*, and thus, ESK-F-6043 and 6044 can be easily distinguished from it.

The genus *Pentalagus* includes only a single living species *P. furnessi*, and no extinct species is known. While ESK-F-6044 is not possible to compare the size because of its unerupted nature, ESK-F-6043 (M^1) is somewhat smaller than recent specimens. The ranges of measurements of M^1 on four modern specimens including those figured in Fig. 3–c and d are 2.4–2.6 mm in length and 3.8–4.0 mm in width. But, other than the size, there is no noticeable difference in morphology, especially the enamel pattern of the internal reentrant fold, between those fossil teeth and modern specimens. Thus, ESK-F-6043 and 6044 are identified to be conspecific with the living one, *P. furnessi*.

Discussion

Geologic age of the fossil-bearing travertine is uncertain as mentioned above. But, the fossil deer *Cervus astylodon* found in the same travertine as *Pentalagus* shows further dwarfness than that of Okinawajima, suggesting its geologic age as rather very late Pleistocene (OTSUKA, 1990). OTSUKA (1990) also suggested that *C. astylodon* migrated to Tokunoshima during the early Middle Pleistocene through the Ryukyu land bridge after the deposition of the Shimajiri Group and before the deposition of the Ryukyu Group. Although the co-occurrence of *C. astylodon* and *P. furnessi* from the same deposits does not necessarily indicate the age of *Pentalagus'* arrival to

Tokunoshima, it makes possible to consider that both species might have arrived at about the same time period through the same migration route.

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