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A NEW SPECIES OF *PLIOPENTALAGUS* (LAGOMORPHA, MAMMALIA) FROM THE PLIOCENE KOBIWAKO GROUP, CENTRAL JAPAN

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ABSTRACT Reported here is the discovery of a new species of leporid mammal from the Pliocene Kobiwako Group in central Japan. *Pliopentalagus okuyamai*, sp. nov., is described based on a partial skull and upper dentition alone. In case of extinct Leporidae, no taxon has been described without the lower dentition, especially the lower third premolar. However, *Pliopentalagus okuyamai* can be distinguished from all known extant and extinct genera (except for *Pliopentalagus*) by characteristics of the palatal bridge and upper dentition alone. Among the genera of the Leporidae, *Pentalagus furnessi* is most closely related to *Pliopentalagus*. However, the extremely deep secondary enamel folds of the internal reentrant and the more squared outline of upper molariform teeth in *Pentalagus furnessi* can be easily distinguished from *Pliopentalagus*. Although the genus *Aztlanolagus* may be congeneric with *Pliopentalagus*, *A. agilis* can be distinguished by the much shallower depth of the secondary enamel folds of upper molariform teeth and much smaller size than *Pl. okuyamai*. Among the known species of *Pliopentalagus*, *Pl. okuyamai* is distinguished by its largest size, the deepest and most densely arranged secondary folds, and the largest length/width ratio of the palatal bridge. *Pl. okuyamai* is the first and oldest record of the family Leporidae in Japan, and may be a possible ancestral form of, or most closely related to, *Pentalagus furnessi*.

KEYWORDS *Pliopentalagus,* new species, Pliocene, Japan

INTRODUCTION

An isolated upper molariform tooth of a leporid was collected, by Mr. Shigemi Okuyama, from the upper part of Ueno Formation of the Kobiwako Group, which is exposed on the river floor of Hattori River in Ohyamada Village (currently Iga City), Mie Prefecture in March 1990 (Fig. 1). In November of the same year, he collected a fragmentary skull of a leporid from the same locality, but it was broken into various parts. Based on the condition of fossil occurrence, components of the material, and relative size and morphology of the left and right teeth, it is assumed that all these fragmentary parts belong to a single skull. The isolated tooth first found is a left upper 4th premolar (P4), and the skull also includes left P4. Based on the general morphology and enamel pattern of the teeth, both the isolated P4 and the skull belong to the same species. Thus, the leporid fossils from this locality represent two individuals of a single species. These specimens were donated to the Lake Biwa Museum (LBM) by Mrs. Kimiyo Okuyama after Mr. S. Okuyama passed away in 2003. Mr. Okuyama was collecting fossils mainly in Mie Prefecture and surrounding area before his death, and his collection was officially donated to the LBM in September, 2010 (Tanimoto and Kitada, 2011). However, the majority of his collection (including those two leporid specimens mentioned above) had already been accessioned by the LBM by early in 2008.

These specimens were briefly studied by Kawamura and Okuyama in 1995 (Kawamura and Okuyama,1995), but no further study was conducted since then. The second author (KT, then Head Curator of the LBM) recommended in 2008 that YT study and describe the specimens. We nearly completed the descriptive part with photos. However, the study was delayed for various reasons in late 2008. The present paper is the completed study after 15 years of silence.

As commonly known among scholars of lagomorph fossils, lower third premolar (p3) is the most important tooth in classification of Leporidae, and p4-m2 are also important in classification of some genera including *Pentalagus* and *Pliopentalagus*. Although the specimens described below do

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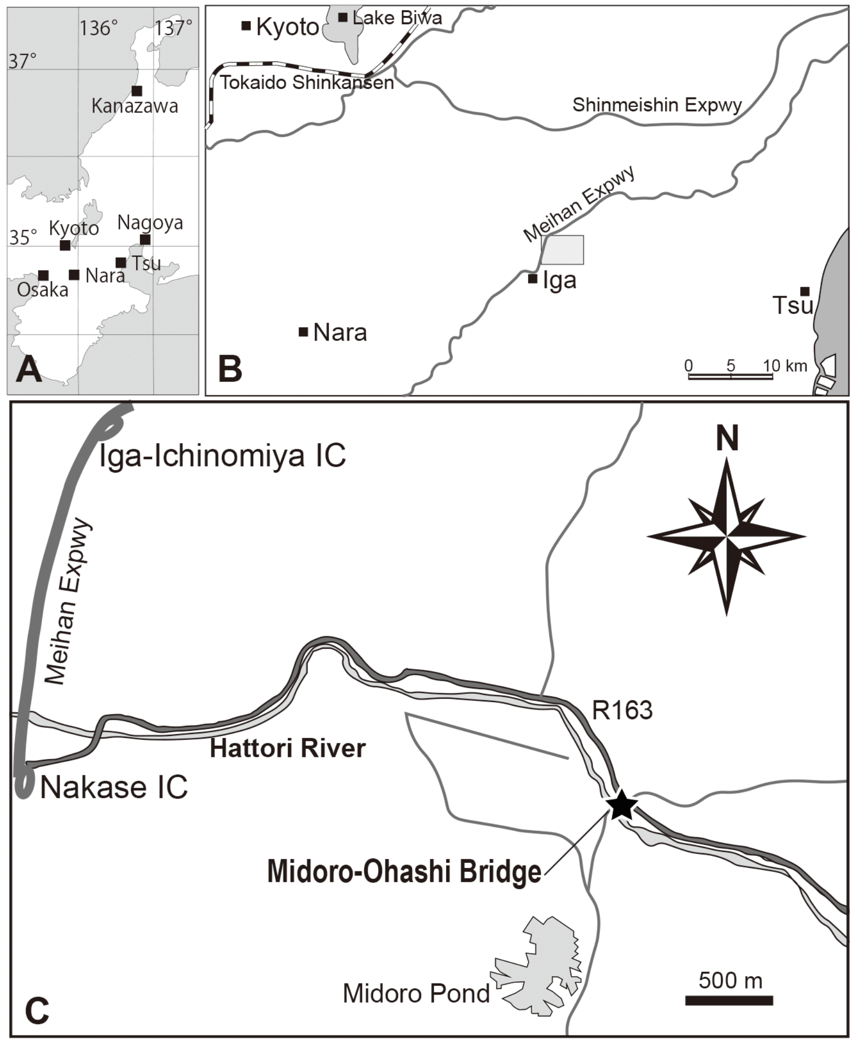

FIGURE 1. Geographic location of the type locality (solid star) of *Pliopentalagus okuyamai*. A, central part of the Honshu, Japan; B, enlargement of between Kyoto and Tsu area; C, enlargement of rectangular grey area near center of B, and the solid star indicates the type locality.

not include any lower dentition, the fragmentary skull preserves nearly complete palatal bridge and most of the upper dentition. Fortunately, both the palatal bridge and enamel pattern of upper dentition of those specimens are characteristic enough to distinguish them from other leporid taxa, and therefore they are described as a new species below.

No leporid fossil has been known from the Tertiary in Japan, and the material described below is the first and oldest record of the family Leporidae in Japan. In addition, it may be a possible ancestral form of, or rather most closely related to, *Pentalagus furnessi* (living Amami Rabbit), rather than of a Chinese species of *Pliopentalagus* described by Tomida and Jin (2009).

METHOD

Measurements of skull were made following Averianov et al. (2000), using a reticule in a Wild M5 stereomicroscope. Measurements of the teeth were also made using a reticule in the same stereomicroscope. For measurement, teeth were held with the portion of the tooth closest to the occlusal surface perpendicular to the table supporting the microscope. Illustrations of the occlusal surface of each tooth were made with the tooth in the same orientation used for measurement. Pencil drawings were made by YT using a camera lucida. Final illustrations were made by tracing these pencil drawings using Adobe Illustrator CS2.

YT examined and collected data (including measurements of teeth and skulls and pencil drawings of the teeth) from all the extant genera of the family Leporidae at The Natural History Museum in London, Museum of Comparative Zoology at Harvard University, and the National Museum of Nature and Science (Japan), and from extinct *Aztlanolagus agilis* at the University of Texas at El Paso. These data are used in comparison with the specimens described in this paper.

Institutional Abbreviations — **LBM**, Lake Biwa Museum, Kusatsu Japan; **NMNS-Z**, National Museum of Nature and Science, Department of Zoology, Tsukuba, Japan

Anatomical Abbreviations — **EAR**, external anterior reentrant; **I**, upper incisor; **IAR**, internal anterior reentrant; **IRF**, internal reentrant fold; **M**, upper molar; **m**, lower molar; **MAR**, main anterior reentrant; **P**, upper premolar; **p**, lower premolar.

SYSTEMATIC PALEONTOLOGY

Order LAGOMORPHA Brandt, 1885
Family LEPORIDAE Gray, 1821
Subfamily LEPORINAE Trouessart, 1880
Genus *PLIOPENTALAGUS* Gureev et Konkova, 1964

Type Species — *Pliopentalagus moldaviensis* Gureev et Konkova, 1964 (in Gureev, 1964), p. 129.

Comments — For detail, see Tomida and Jin (2009).

PLIOPENTALAGUS OKUYAMAI, sp. nov.

(Figs. 2 and 3; Tables 1 and 2)

Holotype — NOTE: The fragmentary skull broken into several parts is considered as a single specimen. However, the LBM catalogued and gave independent numbers to them when they were officially donated, so we give those numbers (below), but we use the term "holotype" (instead of numbers). The catalog numbers consist of ten digits (e.g. 0142001184), and the first 6 digits indicate information like geological age and locations. They are same to all parts mentioned below, but in most cases we use only last 4 digits.

The holotype is a fragmentary skull consisting of following parts: palatal portion with nearly complete palatal bridge and left P2-M1 in place and right P3-P4 (broken but nearly in place) and M1-M2 (broken and dislocated; M2 is only the occlusal tip) (LBM 0142001184), fragmentary premaxillae with left and right broken small I2s (1188), fragmentary left large I1 (1185), left M2 with maxillary fragment (1187), fragmentary right M2 without occlusal surface (part of 1184), and several unidentifiable bone fragments (1189, 1190).

Etymology — In honor of Mr. Shigemi Okuyama who found the holotype and referred specimen and donated them to LBM (through his wife after his death).

Referred specimen — An isolated left P4 with slight weathering near the occlusal surface (LBM 0142001186).

Locality and age — River floor of Hattori River near Midoro O'hashi bridge in Ohyamada Village (currently Iga City), Mie Prefecture, central Japan (Fig. 1). Dark grey mudstone between two tuff beds called Hattori River I and II, upper part of Ueno Formation, Kobiwako Group (Kawamura and Okuyama, 1995), which is correlated near the boundary between Gauss and Gilbert paleomagnetic chrons, about 3.6 Ma (Satoguchi et al., 2005; Satoguchi, 2020).

Diagnosis — Largest known species of the genus. In P3-M2, the secondary folds of IRF are deepest and most densely arranged (counts 10 to 12 on both anterior and posterior walls) among known species of the genus, and the depth of the secondary folds is nearly equal on anterior and posterior walls. The ratio of length/width of the palatal bridge is largest among the known species of the genus and is almost same as that of *Pentalagus furnessi*.

Measurements — See table 1.

Description of holotype — The holotype preserves the palatal bridge, left side of which is nearly complete, while right side is broken somewhat right of the midline; in addition, alveolus of right P3 is unclear (Fig. 2A). Thus, "width" of the palatal bridge (= distance of lingual borders of left and right P3 alveoli; C4 of Fig. 2 in Averianov et al., 2000) is estimated by [the distance between midline, from the suture line of left and right maxillae to the posterior projection of the posterior edge, of palatal bridge and left P3 alveolus] x 2, and it is 13.7 mm. Both anterior and posterior edges of the palatal bridge are preserved on the left side, and the length is measured as 13.84 mm. Thus, the ratio of length/width is estimated as 1.01, which is almost exactly same as that of *Pentalagus furnessi*. Contribution of palatine to the length of palatal bridge is considerable, and proportional contribution of maxilla and palatine to the length is about

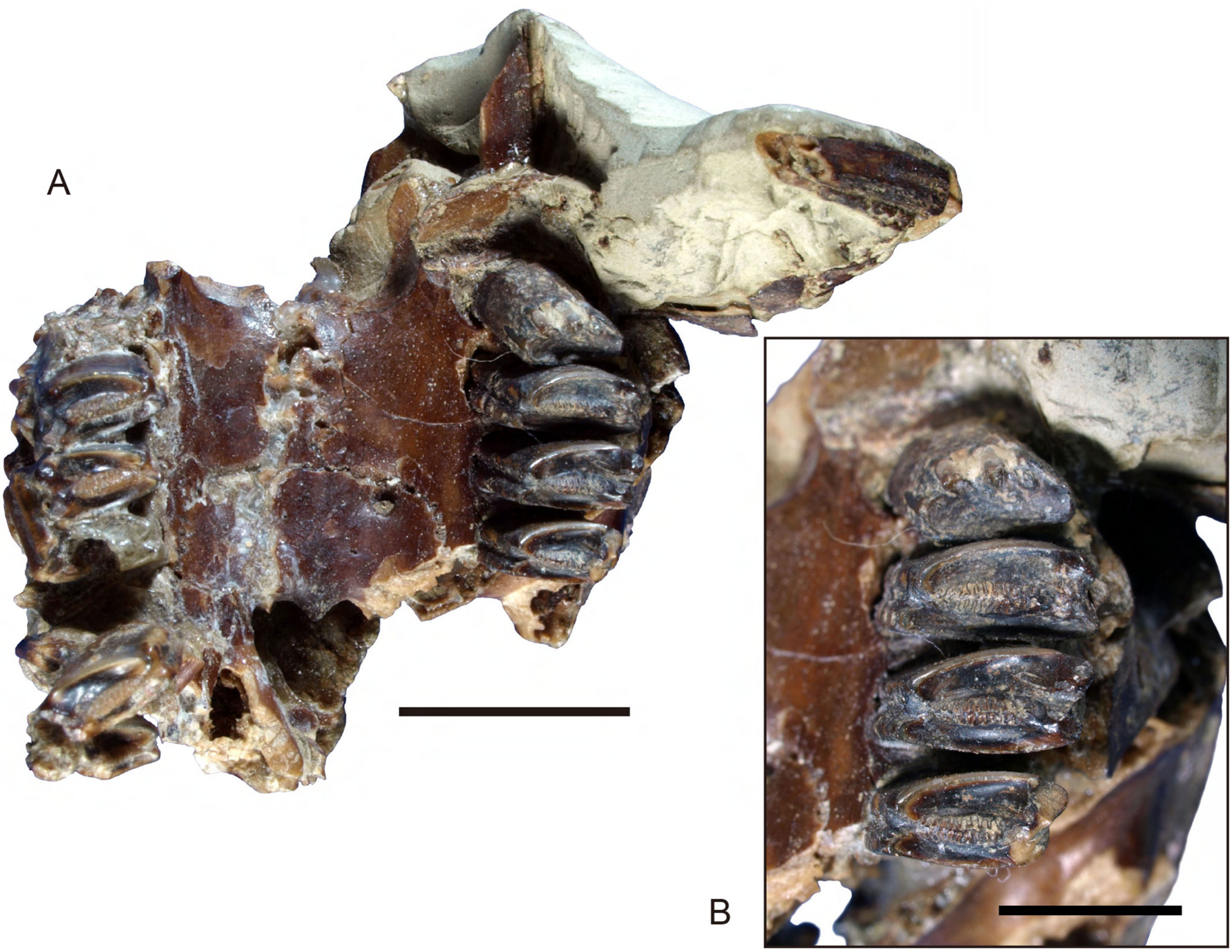

FIGURE 2. Photographs of major portion (LBM 0142001184) of the holotype. **A**, ventral view of the partial skull with palatal bridge, left P2-M1, and right P3-4, tip of M1; **B**, enlargement of occlusal surfaces of left P2-M1. Scale bars are 10 mm and 5 mm for A and B, respectively.

6:5, respectively (Fig. 2A). Posterior part of incisive foramen is observable, and the maximum width of that part is estimated as 9.7 mm, while the width of mesopterygoid fossa is estimated as 5.6-6.0 mm based on the curvature of the posterior edge of palatal bridge. Although the latter is rather inaccurate, it is obvious that the maximum width of incisive foramen is much wider than that of mesopterygoid fossa.

Left and right premaxillae are partly preserved, especially ventral side, and both left and right small second upper incisors are partly observable on the dorsal broken face. A cross section of right one is observable, and it is slightly antero-posteriorly flattened circular in outline with the middle part of the posterior face somewhat swollen. Thin enamel surrounds the tooth (Fig. 3E).

The large first upper incisor (Fig. 3D) is a rounded rectangle (wider than long and more rounded on buccal side), with ratio of about 7 : 10, in cross section, and has a groove on the anterior surface without cement filling. The groove is a wide V shape in cross section, and the apex of the groove lies somewhat medial to the midline of the tooth width (about 45% across the tooth width from the medial edge). Relatively thin enamel covers the anterior face and the anterior 1/3 and anterior half of medial and lateral sides, respectively.

Only one P2 is preserved (Figs. 2B, 3A). The tooth column curves antero-dorsally, then further curves postero-dorsally toward the base of the tooth. P2 is oval in outline in occlusal view, with the posterior face more flattened. There are three reentrant folds on the anterior face, EAR, MAR, and IAR, all of which are filled with cement, and cement further develops

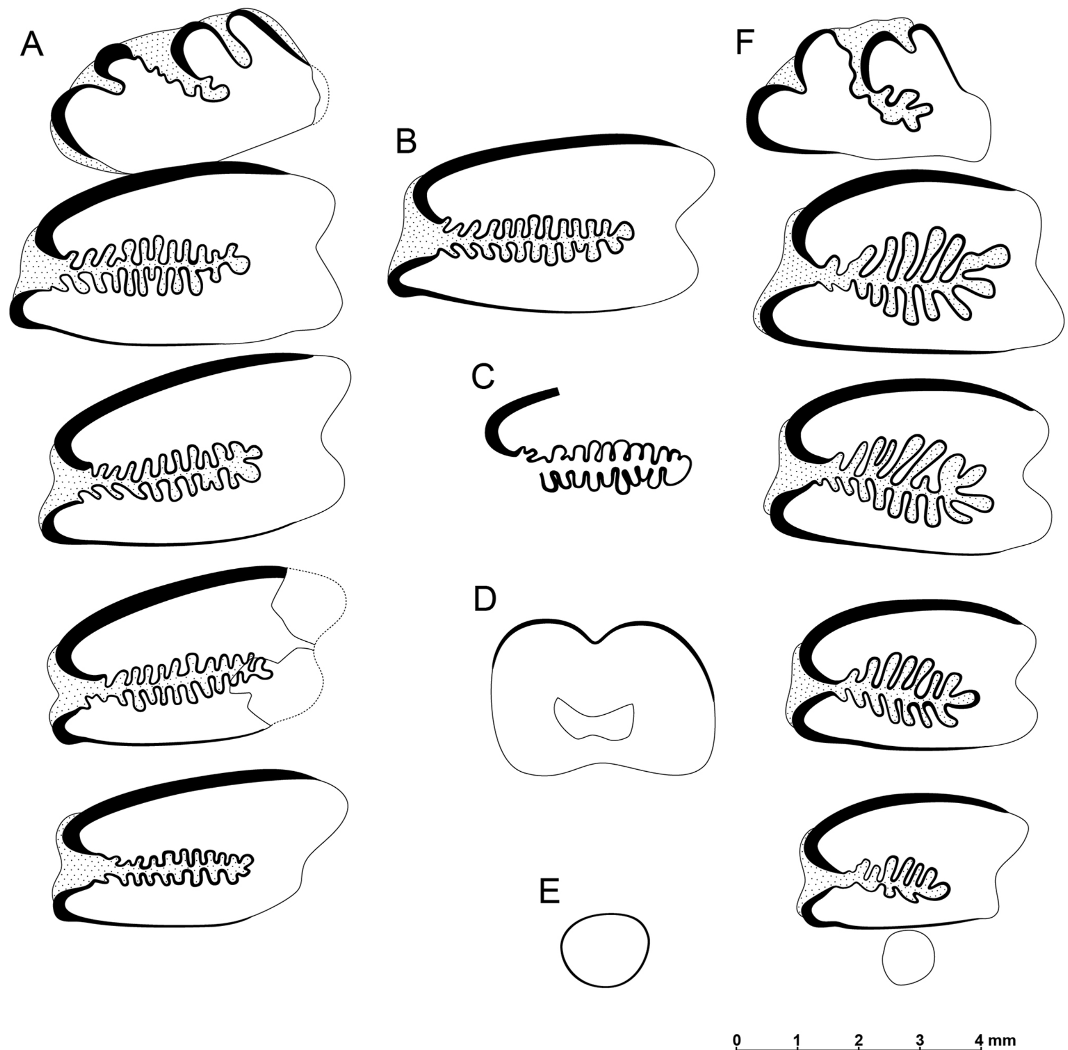

FIGURE 3. Diagrams of the upper dentition of *Pliopentalagus okuyamai* (A to E) and *Pentalagus furnessi* (F). **A**, occlusal surfaces of left P2-M2 of the holotype; **B**, occlusal surface of left P4 of LBM 0142001186; **C**, distal view of right M2 of the holotype; **D**, cross section of left first upper incisor of the holotype; **E**, cross section of left second upper incisor of the holotype; **F**, occlusal surfaces of left P2-M3 of NMNS-Z 1831.

on the anterior face, toward the base of the tooth. MAR is deepest, extends postero-buccally over 60% of the tooth length, and the enamel walls are crenulated. EAR and IAR are both shallower than MAR, extend postero-buccally about 45 and 30% of the tooth length, respectively, and the enamel walls are without crenulations. Thick enamel covers the lingual corner of the tooth and anterior ends of two dentine lobes in the middle, while moderately thick enamel covers the antero-buccal corner.

The holotype includes left and right P3s. P3 is the largest tooth in each cheek tooth row, and the general outline in occlusal view is typical for other leporines. The length/maximum width ratio is 0.55 and 0.53 in left and right P3, respectively, and it is also rather typical. Anterior loph is narrower than posterior at both lingual and buccal ends. Thick enamel covers over 80% of anterior surface of the tooth and the lingual corners of both anterior and posterior lophs. Thin enamel continues on the posterior wall of the posterior loph, reaching across about 2/3 the tooth width. Deep IRF is locating somewhat posterior to the midline of the tooth, reaching nearly 3/4 of the way across the tooth width. The secondary enamel folds are very deep (but still shallower than *Pentalagus furnessi*) on both anterior and posterior walls, and both walls are aligned very closely to

TABLE 1. Measurements of the teeth of holotype and LBM 0142001186. (*) indicates to be measured on the tooth shaft

			Length	Ant. Width	Post. Width	Max. width
Holotype						
	Left	I1	2.64			3.76
		P2	2.16	4.58		
		P3	3.08	5.08	5.58	5.58
		P4	3.12	5.08	5.08	5.48
		M1	2.84	5.00	4.58	5.06
		M2	2.56	4.92	4.12	5.17
	Right	I2	1.20			1.44
		P3	3.16	5.42	6.00	6.00
		P4	3.16	5.33	5.42	5.62
		M1	2.84	5.25	4.92	5.42
		M2	2.52			
LBM 0142001186						
	Left	P4*	3.04	5.25	5.17	5.72

TABLE 2. Comarisons of the palatal bridges among *Pliopentalagus*, *Pentalagus*, and *Aztlanolagus*. (*) indicates estimated value

Taxa	Numbe of specimens	Length of palatal brige (C4) in range	Distance of P3s alveoli (C5) in range	Ratio C4/C5 in average
Pliopentalagus huainanensis	1	8.21	9.67*	0.85
Pliopentalagus dajushanensis	9	7.48-8.96	9.89-11.29	0.74
Pliopentalagus anhuiensis	2	5.69-6.01	8.99-9.71	0.63
Pliopentalagus okuyamai	1	13.84	13.7*	1.01
Pentalagus furnessi	7	10.60-12.90	10.93-12.54	1.02
Aztlanolagus agilis	1	6.68	7.47	0.89

each other. Ratio between maximum total length of both anterior and posterior folds and the tooth length is ca. 33% in left P3. In addition, the secondary enamel folds are densely arranged; they count 11 on the anterior wall and 11 (there is a twelfth small one) on the posterior wall in left P3 (Fig. 3A); 12 and 11 in right P3. The depth of the secondary folds is about the same on the anterior and posterior walls.

Morphology of P4 through M2 is quite similar to that of P3 in general, and the following description includes mainly differences between each tooth and P3. The holotype also includes left and right P4s. P4 is the second largest tooth in each cheek tooth row, and the length/maximum width ratio is 0.57 and 0.56 in left and right P4, respectively. Anterior loph is narrower than posterior loph lingually, while the former is slightly wider than the latter buccally. Thick enamel covers nearly 90% of anterior surface of the tooth, while thin enamel continues on the posterior wall of the posterior loph, reaching over 80% of the tooth width. Secondary enamel folds are slightly shallower than P3, and the ratio between maximum total length of both anterior and posterior folds and the tooth length is ca. 30% in left P4. Enamel folds count 11 on the anterior wall and 10 on the posterior in left P4; 10 and 11 in right P4. The depth of the secondary folds is about the same on the anterior and posterior walls, as in P3.

In M1, the length/maximum width ratio is 0.56 and 0.52, left and right, respectively. Anterior loph is only slightly narrower than posterior loph lingually, while the former is obviously wider than the latter buccally, thus the anterior loph is clearly wider than the posterior. Thin enamel covering posterior wall of the posterior loph reaches nearly 80% of the width of posterior loph (or ca. 73% of the maximum tooth

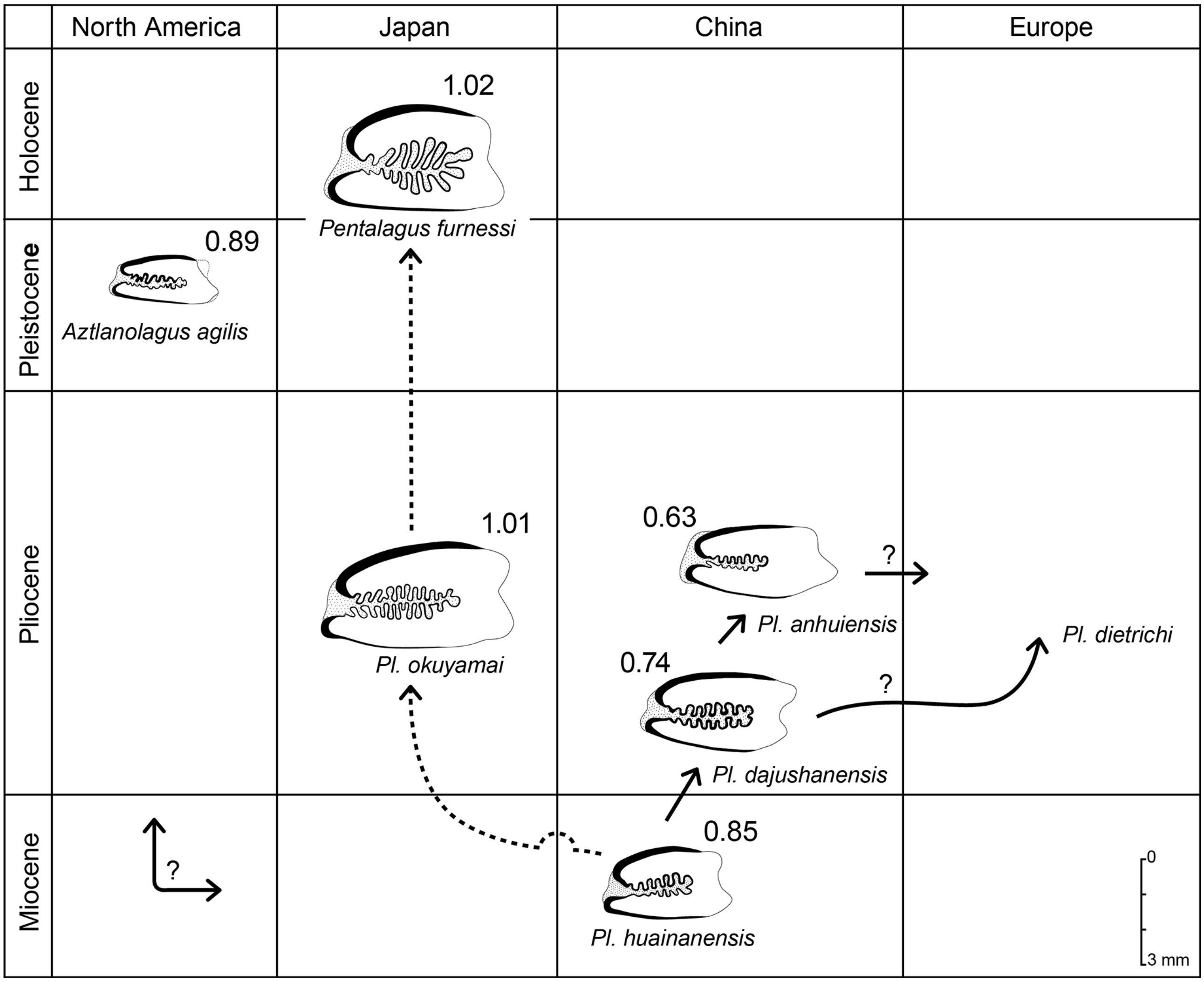

FIGURE 4. Proposed phylogeny of *Aztlanolagus agilis*, *Pliopentalagus* spp, and *Pentalagus furnessi*. Time and place of the *Aztlanolagus*/*Pliopentalagus* transition are unkown so far. Number above each tooth illustration indicates average of width/length ratio of the palatal bridge for each.

width). Secondary enamel folds are slightly shallower than P4, but tooth length is also somewhat shorter, so the ratio between maximum total length of both anterior and posterior folds and the tooth length in left M1 (ca. 29%) is almost same as in left P4. Secondary enamel folds are still densely arranged and count 11 on the anterior wall and 12 on the posterior wall in left M1; 10 and 10 in right M1.

In left M2, the length/maximum width ratio is 0.50, while it is not available in right M2 because of breakage. Anterior loph is slightly narrower than posterior loph at lingual end, while the former is much wider than the latter at buccal end, thus the anterior loph is definitely wider than posterior. Thick enamel covers over 90% of anterior surface of the tooth width, while thin enamel covers nearly 80% of the posterior wall. Secondary enamel folds are somewhat shallower than in M1, and the ratio between maximum total length of both anterior and posterior folds and the tooth length in left M2 is ca. 26%, somewhat less than in left M1; but they are still densely arranged and count 11 on the anterior wall and 10 on the posterior wall in left M2. Right M2 is broken into two parts, and the enamel pattern of distal end is visible on the isolated part (Fig. 3C). The secondary enamel crenulations are already being formed but enamel deposition is not yet complete at this stage and cement is not yet deposited.

Description of Referred Specimen — This tooth fragment is somewhat weathered, with some thick enamel and dentine around the tooth missing on and near the occlusal surface. However, the tooth is otherwise normal and the illustration (Fig. 3B) is made with the enamel estimated based on the normal part of the tooth, which is visible through a stereo-microscope.

General outline of occlusal surface including the fact that anterior loph is narrower than posterior loph at lingual end while the former is slightly wider than the latter at buccal end, indicates that LBM 0142001186 is a left P4 of a leporine. Compared to P4 of the holotype, LBM 0142001186 is similar in size, but relative width is slightly greater (the length/maximum width ratio is 0.53). Thick enamel covers about 90% of anterior surface of the tooth and the lingual corners of both anterior and posterior lophs. Thin enamel continues posterior wall of the posterior loph, reaching about 80% of the width of the loph. Deep internal reentrant fold is somewhat posterior to the midline of the tooth, reaching about 3/4 way across the tooth width. Secondary enamel folds are as deep as in the holotype, and the ratio between maximum total length of both anterior and posterior folds and the tooth length is ca. 29%. Enamel folds count 12 (13 counting the first tiny one) on the anterior wall and 11 on the posterior. The depth of the secondary folds is about the same on the anterior and posterior walls. The above detailed description strongly suggests that LBM 0142001186 and the holotype represent the same species.

DISCUSSION

As commonly recognized among scholars of lagomorph fossils, lower third premolar (p3) is the most important tooth in classification of the Leporidae, and p4-m2 are also important in classification of some genera. Probably, as far as we know, no taxon of the family has been described based on the upper dentition alone. However, combinations of the following characters among the upper dentition of the Leporidae can identify the specimens described above as the genus *Pliopentalagus*: (1) presence/absence of cement in the groove on I1, (2) number of anterior reentrants on P2, (3) presence/absence of crenulation and the depth of MAR on P2, (4) depth of IRF in P3-M1, (5) condition of enamel walls of IRF in P3-M1, and (6) number of secondary enamel folds (both anterior and posterior) of the IRF on P3-M1.

Among the extant and extinct genera of the Leporidae, *Pentalagus furnessi* is morphologically the most closely related taxon to the genus *Pliopentalagus*. However, the depth of the secondary folds of IRF of P3-M1 is much deeper in *Pentalagus* than *Pliopentalagus* in general, and number of secondary folds in P3-M1 is obviously fewer in *Pentalagus furnessi* than *Pl. okuyamai*, at least (Fig. 3A, F). Also, general outline of P3-M1 is more squared (antero-posteriorly long) in *Pentalagus* while that of *Pliopentlagus* is more rectangular (antero-posteriorly short) (Fig. 3). Thus, we conclude that *Pl. okuyamai* is a species of the genus *Pliopentalatus*, not the genus *Pentalagus*.

The genus *Aztlanolagus* known from North America may be con-generic with *Pliopentalagus* (Tomida and Jin, 2004, 2008). Discussion of these two genera and *Pentlagus*, including phylogenetic and paleogeographic relationships, is currently being prepared as a separate paper by YT. Therefore, we note morphological differences between *Pl. okuyamai* and *A. agilis* alone in this paper. The secondary folds of IRF of P3-M1 in *A. agilis* are obviously shallower than in *Pl. okuyamai*, especially the posterior secondary folds which are even shallower than the anterior. In addition, the size of the teeth is much smaller than *Pl. okuyamai*.

Four other species are recognized in the genus *Pliopentalagus*: *Pl. dietrichi*, *Pl. anhuiensis*, *Pl. dajushanensis*, and *Pl. huainanensis*. (Daxner and Fejfar, 1967; Tomida and Jin, 2009). In terms of the size of upper P3-M1, these four species are all obviously smaller than *Pl. okuyamai*. Also, the depth and number of the secondary enamel folds of IRF are shallower and fewer, respectively, than *Pl. okuyamai* (Fig. 4).

Other than the largest tooth size and very deep and densely arranged secondary enamel folds of P3-M1 in *Pl. okuyamai* among the species of the genus, another characteristic feature of the species is the extremely long palatal bridge. As described above, the length (C4) and width (C5) of the palatal bridge are 13.84 and 13.7 mm, respectively, and the ratio of C4/C5 is 1.01, which is almost exactly same ratio as in *Pentalagus furnessi* (Table 2). On the other hand, the ratio in other species (as far as known) of the genus is less than 0.85, and that of *Aztlanolagus agilis* is 0.89 (Table 2). In addition, the ratio becomes smaller from the older species to younger species in Chinese lineage, while it is large in *Pl. okuyamai* (Fig. 4).

As described above, it is obvious that the maximum width of incisive foramen is much wider than that of mesopterygoid fossa in *Pl. okuyamai*, while the former is narrower than the latter in *Pentalagus furnessi*, thus the relationships of the two widths are opposite in these two taxa. Parenthetically speaking, the maximum width of incisive foramen is also wider than that of mesopterygoid fossa in *Pl. dajushanensis*, but the difference is smaller. In addition, the proportional contributions of the maxilla and palatine to the palatal bridge length is about 6:5, respectively, in *Pl. okuyamai*, while it is about 8:2 in *Pentalagus furnessi*. Thus, these taxa are dissimilar in the two characteristics mentioned above.

Combining all the characteristics mentioned above, we propose phylogenetic relationships among these taxa (Fig. 4). We do not know where and when *Aztlanolagus*/*Pliopentalagus* originated, but *Pl. huainanensis* is the oldest and most primitive species within the Asian lineages, and *Pl. dajushanensis* and *Pl. anhuiensis* gradually evolved within China (Tomida and Jin, 2009). Sometime before 3.6 Ma, *Pl. huainanensis* or similar species migrated to Japan and evolved into *Pl. okuyamai* by 3.6 Ma with the characteristics of larger size, deeper and densely arranged secondary folds of IRF of P3-M1, and the length/width ratio of palatal bridge toward 1. If the secondary folds of IRF of P3-M1 deepen, and general outline of P3-M1 becomes squared (antero-posteriorly longer), the new species becomes more similar to *Pentalagus furnessi*. But, how or why the relationships in widths of incisive foramen and mesopterygoid fossa have changed is unclear so far. At any rate, we conclude that *Pl. okuyamai* may be a possible ancestral form of, and at least most closely related to *Pentalagus furnessi*.

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AUTHOR CONTIBUTIONS

YT described the original specimens, made comparisons with other taxa, and drafted the manuscript. KT arranged this project and took photos. Both authors edited the manuscript.

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