



AZTLANOLAGUS REVISITED AND THE DYNAMIC EVOLUTION OF *PLIOPENTALAGUS* (LEPORIDAE, LAGOMORPHA) IN THE HOLARCTIC REGION

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Abstract: The genus *Aztlanolagus* from North America is synonymized with *Pliopentalagus* based on similar morphology of dental characters including (1) general form of five reentrant angles and outline of p3, (2) an enamel lake at the position of PIR, (3) general form of enamel crenulations of the anterior wall of the talonid on p4–m2, and (4) an AER on p4–m2 on some specimens. However, the species *A. agilis* is valid because of its much smaller size. The general morphology and size of this species, transferred to *Pliopentalagus*, did not change for about the last 2.5 million years. Three Asiatic species of *Pliopentalagus* (*Pl. huainanensis*, *Pl. dajushanensis*, and *Pl. anhuiensis*, from geologically older to younger) were described from the latest Miocene (ca. 6 Ma) to Late Pliocene (ca. 3 Ma) at Dajushan in Anhui Province, China. These taxa represent a gradually evolving lineage, an example of phyletic gradualism. *Pliopentalagus okuyamai* was recently described based on a fragmentary skull with upper dentition from ca. 3.5 Ma deposits in Japan and represents a possible ancestral form of the living type species, *Pentalagus furnessi*. Fossil *Pliopentalagus dietrichi* is known from the Early Pliocene in Europe and likely evolved from Chinese *Pl. dajushanensis*. However, *Pl. dietrichi* lacks an enamel lake on p3 and an AER on p4–m2; this assumes that the ancestral population dispersing to Europe probably did not have a gene controlling the appearance of an enamel lake on p3 and an AER on p4–m2. Thus, *Pliopentalagus* diversified and dispersed widely across the Holarctic region over the last 6 million years, disappeared near the end of the Pleistocene, and left a single descendant, *Pentalagus furnessi* in Japan.

Key words: *Pliopentalagus*, *Aztlanolagus*, *Pentalagus*, Leporidae, evolution, Holarctic region

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Introduction

The genus *Pliopentalagus* GUREEV et KONKOVA in GUREEV, 1964 was first named by Gureev and Konkova in Gureev (1964). Fejfar (1961) described *Alilepus dietrichi* FEJFAR, 1961, which was later combined with the genus *Pliopentalagus*. Daxner and Fejfar (1967) redescribed *Pl. dietrichi* (FEJFAR, 1961) in detail. However, no major study on *Pliopentalagus* was published until 2009, when three species (one revised and two newly described) of the genus *Pliopentalagus* demonstrated that they formed an evolutionary lineage, an example of phyletic gradualism

(Tomida and Jin 2009). While studying those three species of the genus, two of us (YT and CJ) recognized that *Aztlanolagus agilis* RUSSELL et HARRIS, 1986 from North America is very similar in morphology to the oldest known species (*Pl. huainanensis* JIN, 2004) of the genus from the Late Miocene of China. Because of this, YT reexamined all the materials of *A. agilis* stored at UTEP (Russell and Harris 1986), and at UALP and TMM (Winkler and Tomida 1988). Recently, another species of the genus (*Pl. okuyamai* TOMIDA et TAKAHASHI, 2023) was newly described based on a fragmentary skull (without lower dentition) from the middle Pliocene of Japan (Tomida and Takahashi 2023).

Looking at all these species together in terms of their detailed morphology, geologic age and geographical distributions, a picture emerges of the dynamic evolution of the genus *Pliopentalagus*. This paper discusses this transformation and proposes a scenario for the dynamic evolution of *Pliopentalagus*.

Material and methods

For the reviews and discussion, we used data including descriptions, measurements, and illustrations from the published literature. For example, data on three species of *Pliopentalagus* from Dajushan in Anhui Province, China, are from Tomida and Jin (2009). Two of us reviewed all data on *Aztlanolagus agilis*: YT examined essentially all teeth, skulls and mandibles of *A. agilis* from Dry Cave, New Mexico, and those referred to this taxon from Anthony Cave, New Mexico and adjacent Texas, U-Bar Cave, New Mexico, and Jimenez Cave, southern Chihuahua, Mexico (see Russell and Harris 1986, for detail); YT and AJW also reexamined all materials from Fyllan Cave, Texas, and a single p3 from 111 Ranch, Arizona in 2003, 2006, and 2008. YT and CJ also reexamined all the material of *Pliopentalagus nihewanensis* CAI, 1989 from the Late Pliocene of Hebei Province (Cai 1989) and *Pliopentalagus progressivus* LIU et ZHENG, 1997 from the Late Pliocene or Early Pleistocene of Henan Province (Liu and Zheng 1997) in 2004.

For the length/width ratio of the palatal bridge, the length is the minimum distance between incisive foramen and posterior border of the palatal bridge, and the width is the distance between left and right p3 alveoli.

Measurements of the teeth were made using the scale of the stereo-microscope (Wild M5), with each tooth set vertically as much as possible. Illustration of the occlusal surface of each tooth is also made after setting it vertically: the total length of the full dentition in illustrations may not be exactly the same as that of full dentition in

direct measurement. Pencil line drawings were made by YT using camera lucida, and the final illustrations were completed using Adobe Illustrator CS2 based on those pencil drawings.

Anatomical abbreviations

Tooth abbreviations include: p, lower premolar; m, lower molar; P, upper premolar; M, upper molar; numeral after p, m, P, and M indicates the position of the tooth. Abbreviations for reentrant angles of p3 and p4–m2 used in this paper are shown in Text-fig. 1.

Institutional and other abbreviations

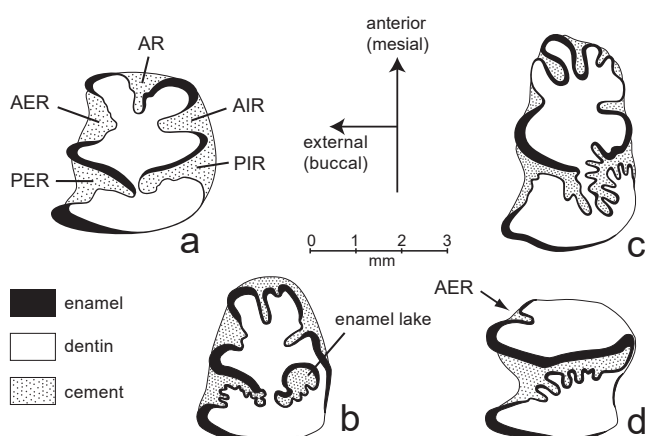
IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Science, Beijing, China; MNM – Museum of New Mexico (currently housed at UTEP); NMNS-M – Department of Mammalogy, National Museum of Nature and Science, Tsukuba, Ibaraki, Japan; TMM – Texas Memorial Museum Collection (now part of the Texas Vertebrate Paleontology Collections, Jackson School Museum of Earth Sciences), University of Texas at Austin, Texas, USA; UALP – Laboratory of Paleontology, University of Arizona, Tucson, Arizona, USA; UTEP – Laboratory for Environmental Biology, University of Texas at El Paso, Texas, USA.

ka – thousand years ago; Ma – million years ago.

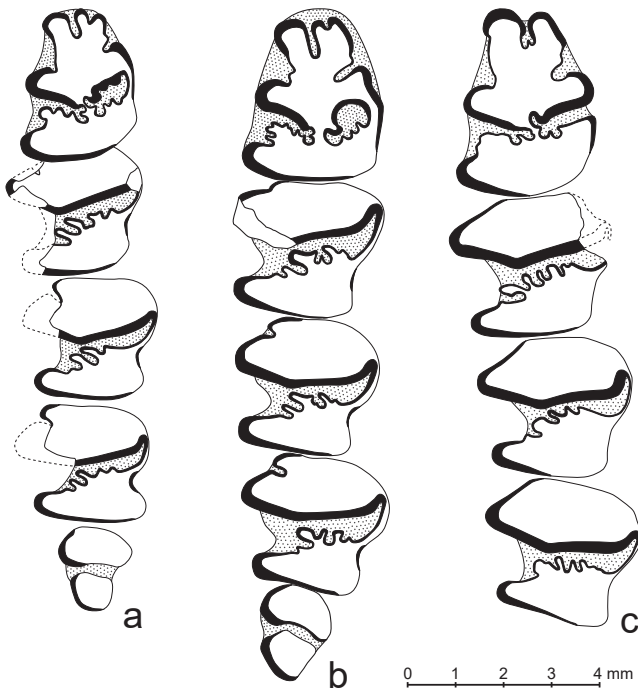
Three species of *Pliopentalagus* from Anhui Province, China

Numerous specimens of *Pliopentalagus* were found by one of us (CJ) from three cave deposits within a large limestone mountain (Dajushan), in Anhui Province, China, during the late 1990's. Each cave is located at a different altitude, and the caves at higher altitude are geologically older because the entire Dajushan was uplifted multiple times. Based on the biochronology of mammalian fossil taxa found with *Pliopentalagus*, they are estimated to date from the latest Miocene (ca. 6 Ma), Early Pliocene (ca. 5–4 Ma), and Late Pliocene (ca. 3 Ma) (Tomida and Jin 2002).

The following morphologic changes were observed on samples of skulls, mandibles and dental remains, from older to younger geologic age: (1) size of each tooth on average increases gradually, (2) enamel crenulations of PER and PIR become deeper gradually, (3) AR becomes deeper and more complicated, (4) frequency of presence of an enamel lake at the position of PIR on p3 changes from 100% to 33% (18% in recent *Pentalagus*), (5) frequency of presence of an AER on p4–m2 changes from 71% to 29% (0% in recent *Pentalagus*) (Tab. 1) (Tomida and Jin 2009). Because the size of each tooth from the three localities overlaps widely, it is impossible to distinguish the specimens from each locality by size. However, based on those characters mentioned above (1 to 5), the populations of each locality were described as different species: *Pl. huainanensis* (this species was originally described by Jin (2004), but revised by Tomida and Jin (2009)), *Pl. dajushanensis*, and *Pl. anhuiensis*, from oldest to youngest (Tomida and Jin 2009; Text-fig. 2). This series of three species is considered to provide an example of sympatric phyletic gradualism (alternative to punctuated equilibria; Eldredge and Gould 1972).



Text-fig. 1. Occlusal enamel pattern of lower cheekteeth in Leporidae and terminology of reentrant angles. **a:** Hypothetical left p3; AR – anterior reentrant angle, AER – antero-external reentrant angle, AIR – antero-internal reentrant angle, PER – postero-external reentrant angle, PIR – postero-internal reentrant angle. **b:** Left p3 of *Pliopentalagus*, an example of PIR as an enamel lake. **c:** Left p3 of *Pentalagus furnessi*. **d:** Left p4 of *Pliopentalagus*, an example of AER, antero-external reentrant angle.



Text-fig. 2. Occlusal pattern of lower cheekteeth of three species of *Pliopentalagus* from Dajushan in Anhui Province, China. a: *Pl. huainanensis*, left p3–m3 (IVPP-V10817.2). b: *Pl. dajushanensis*, left p3–m3 (holotype, IVPP-V14180.3). c: *Pl. anhuiensis*, left p3–m2 (holotype, IVPP-V15328.1).

Based on characters 1 to 5 (above), the morphologic transition through time observed in the three species of *Pliopentalagus* from Dajushan seems to approach the morphology seen in recent *Pentalagus*. However, it is apparent that there is a gap between *Pliopentalagus* and *Pentalagus* in the following characters: (1) smaller size, (2) general outline of p3, (3) more complicated enamel crenulations on each reentrant angle of p3, especially PIR, and (4) degree of complication and depth of enamel crenulations/folds of the anterior wall of the talonid on p4–m2 (Text-fig. 3). Furthermore, another character contradicts a supposed lineage from the Dajushan species to *Pentalagus*: that is the length/width ratio of the palatal bridge. It decreases from 0.85 of *Pl. huainanensis*, 0.74 of *Pl. dajushanensis*, to 0.63 of *Pl. anhuiensis*, while the average ratio in recent

Pentalagus is 1.02. Thus, the evolutionary trend among the three Chinese species suggests *Pl. anhuiensis* could not be a direct ancestor to *Pentalagus* (Tab. 1).

Aztlanolagus revisited

Aztlanolagus is *Pliopentalagus*

Aztlanolagus agilis was first described by Russell and Harris in 1986, based on numerous materials from the Rancholabrean land-mammal age (Wisconsinan age, ca. 30 ka) in southern New Mexico, western Texas, and northern Mexico (Russell and Harris 1986). They compared *A. agilis* with *Nekrolagus progressus* HIBBARD, 1939 in detail. They also mentioned some similarity with Old World leporines, including *Pentalagus* LYON, 1904, but suggested *Nekrolagus* HIBBARD, 1939 as showing the greatest similarity with *Aztlanolagus* RUSSELL et HARRIS, 1986, mainly because PIR is represented by the enamel lake, rather than the open reentrant angle.

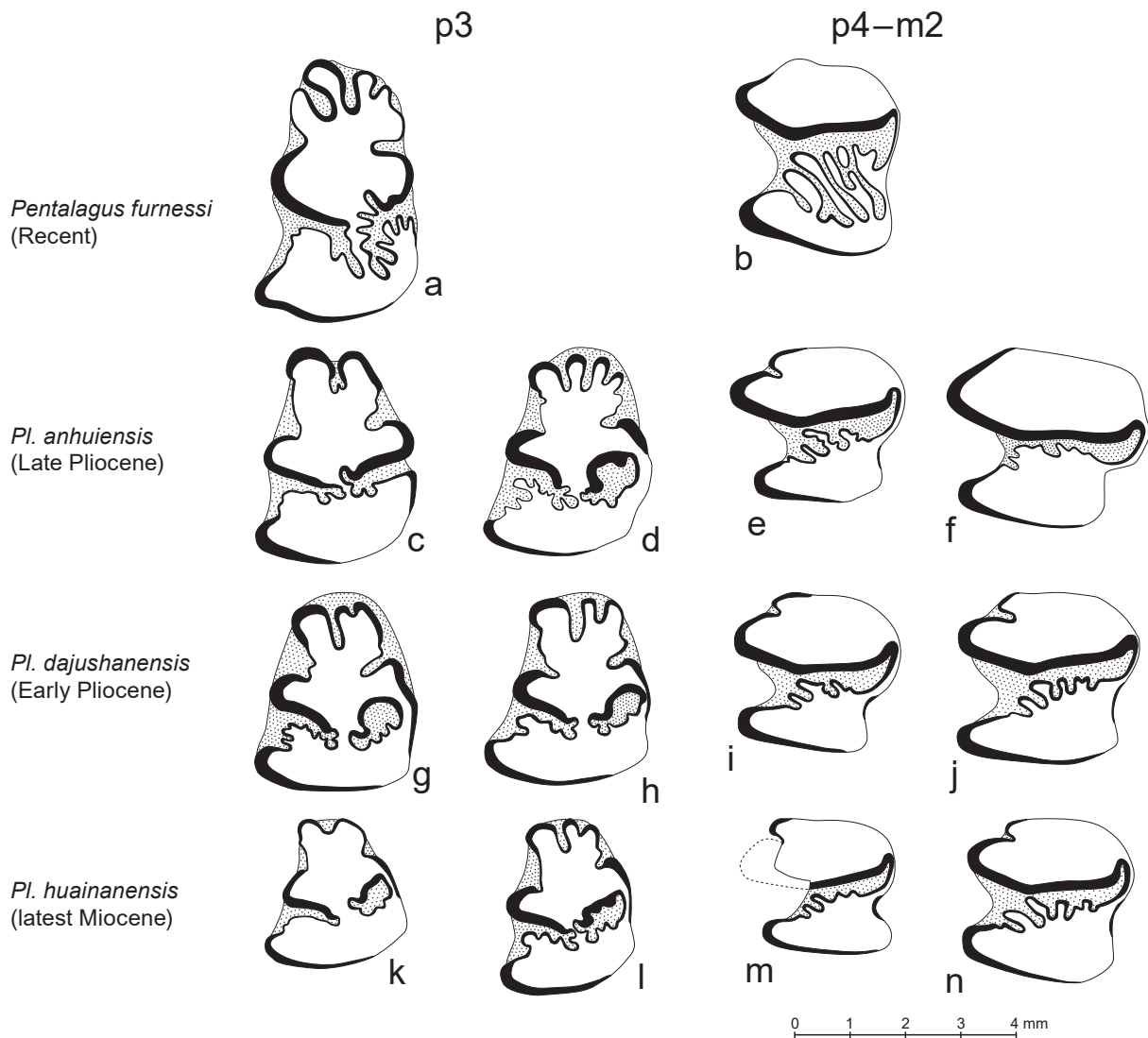
Winkler and Tomida (1988) described additional specimens of *A. agilis*, from Fyllan Cave (Irvingtonian land-mammal age; >0.73 Ma), central Texas, and from 111 Ranch (Blancan land-mammal age; ca. 2.5 Ma), southeastern Arizona. They extended the geographic range of this species to central Texas and Arizona, and the temporal range to ca. 2.5 Ma. These authors also agreed with Russell and Harris (1986) that *Aztlanolagus* is most closely related to *Nekrolagus*.

However, while studying the specimens of *Pliopentalagus* spp. from Dajushan, in Anhui Province, China, CJ and YT recognized that the enamel patterns of not only p3 but also p4–m2 are quite similar to *Aztlanolagus*, and that one of the p4–m2 specimen of *Aztlanolagus* possesses a small AER (Winkler and Tomida 1988: fig. 2B) as seen in *Pliopentalagus* from Dajushan.

In fact, except for the size, *Pl. huainanensis* and *Aztlanolagus agilis* are very similar in (1) general form of five reentrant angles and general outline of p3, (2) all the specimens possess an enamel lake at the position of PIR (as demonstrated below), (3) general form of enamel crenulations of the anterior wall of the talonid on p4–m2, and (4) some specimens possess an AER on p4–m2 (see Text-figs 3, 4). Thus, we propose that *Aztlanolagus* be

Table 1. Comparison of the frequency of an enamel lake at the position of PIR on p3 and AER on p4–m2, and the average length/width ratio of the palatal bridge among five species of *Pliopentalagus* and *Pentalagus furnessi*.

Taxa (Geologic age)	p3		p4–m2		Palatal bridge	
	N: adult specimens	Frequency of enamel lake	N: adult specimens	Frequency of AER	N: adult specimens	Length/width ratio
<i>Pentalagus furnessi</i> (Recent)	22	18.2 %	127	0 %	7	1.02
<i>Pl. anhuiensis</i> (Late Pliocene)	6	33.3 %	24	29.2 %	2	0.63
<i>Pl. dajushanensis</i> (Early Pliocene)	31	83.9 %	119	65.5 %	9	0.74
<i>Pl. huainanensis</i> (latest Miocene)	5	100 %	17	70.6 %	1	0.85
<i>Pl. dietrichi</i> (Early Pliocene)	7	0 %	25	0 %		
<i>Pl. agilis</i> (Wisconsinan, ca. 30 ka)	63	100 %	138	14.5 %	1	0.89
<i>Pl. agilis</i> (Irvingtonian, >0.73 Ma)	7	100 %	10	10 %		
<i>Pl. agilis</i> (Blancan, ca. 2.5 Ma)	1	100 %				



Text-fig. 3. Comparisons of enamel patterns in p3 and p4-m2 among three species of *Pliopentalagus* from China and recent *Pentalagus furnessi* from Japan. a: NMNS-M12938; b: p4 of NMNS-M12938; c: IVPP-V15328.1 (holotype); d: IVPP-V15328.3; e: m1 of IVPP-V15328.3; f: m1 of IVPP-V15328.6; g: IVPP-V14180.3 (holotype); h: IVPP-V14180.5 (reversed); i: m1 of IVPP-V14180.3 (holotype); j: p4 of IVPP-V14180.17; k: IVPP-V10817.1 (holotype); l: IVPP-V10817.2; m: m2 of IVPP-V10817.2; n: right p4 of IVPP-V10817.5 (reversed).

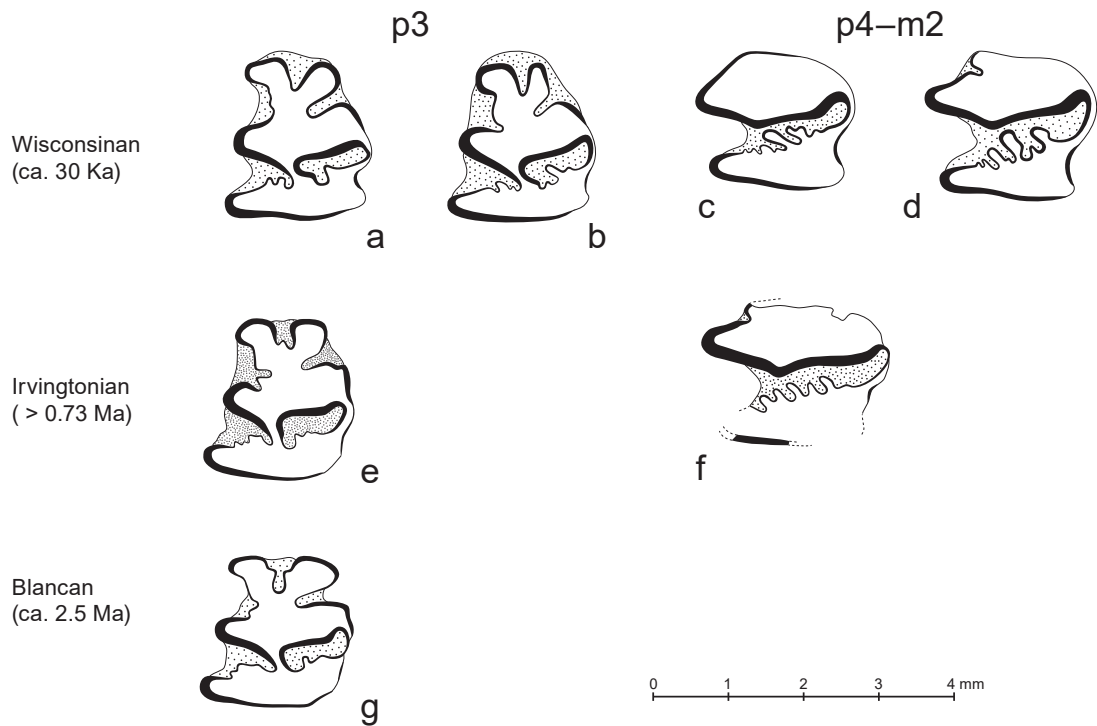
synonymized with *Pliopentalagus*, but retain *A. agilis* as a valid species because of its obvious smaller size.

Reexamination of the original material of *A. agilis*

The specimens reexamined are mentioned in the Material and methods section above. We follow general descriptions of *A. agilis* by Russell and Harris (1986) and do not repeat them here. We noted the condition of PIR (either enamel lake or open reentrant angle) on p3 and noted the presence/absence of AER on p4-m2. Among the UTEP and MNM specimens, out of 64 adult p3s, 63 possess enamel lakes at the position of PIR, while one (MNM 5689-6-29) possesses PER and the enamel lake connected, thus showing the “*Lepus*” pattern (Russell and Harris 1986: fig. 1D). However, this specimen does not have an open reentrant angle. If this specimen is counted as having an enamel lake, the frequency of the specimen with an enamel lake at the position of PIR is 100% (Tab. 1). In addition, two specimens (MNM 5689-78-18 and 5689-98-1) show an enamel lake at the position

of AIR (as described by Russell and Harris 1986: fig. 2E). Most subadult specimens (10 out of 11) also possess the enamel lake at the position of PIR. The occlusal surface of one subadult specimen (MNM 9366-9946-12) shows that the trigonid and talonid are separated, but the bottom surface has the enamel lake as in adult teeth.

In terms of p4-m2, it is easy to identify their positions if they are in situ on the mandible. Even with isolated teeth, it is often possible to identify tooth position when the curvature of the tooth is considered: p4 is almost perpendicular, m1 is somewhat curved posteriorly, and m2 is more curved posteriorly. Of 138 teeth of p4-m2 (including those in situ on the mandible and isolated), 20 possess an AER, about 14.5% of the teeth (Tab. 1). However, the ratio differs among the tooth position: 13 out of 53 p4s (ca. 24.5%), 5 out of 49 m1s (ca. 10.2%), and 2 out of 36 m2s (ca. 5.6%). There is a tendency for all p4-m2 of a single mandible to show (UTEP 1-1202) or not show (MNM 5689-6-29) the AER (Russell and Harris 1986: fig. 1C, D). This is not always the



Text-fig. 4. Comparisons of enamel patterns in p3 and p4–m2 of *Pliopentalagus agilis* from three localities. a: MNM 5689-73-2; b: MNM 5689-153-279; c: m1 of MNM 5689-6-29; d: m1 of UTEP 1-1202 (holotype); e: TMM 40682-76A (cut-and-polished surface); f: TMM 40682-76B (cut-and-polished surface); g: UALP 15975 (reversed).

case: in specimen MNM 5689-98-1, p4 possesses an AER, while m1 does not.

Another important character of *A. agilis* is the length/width ratio of the palatal bridge. Only one specimen (MNM 5689-1-45) has a complete palate. Although Russell and Harris (1986: 636) mention the ratio of length to width being 1.00 in the text, their illustration shows the ratio at about 0.91. YT measured the original specimen and obtained 0.89 (Tab. 1).

Reexamination of all *A. agilis* from the Irvingtonian and Blancan age localities

Considering material from Fyllan Cave (Irvingtonian), all available specimens are isolated teeth, and the surface of most of the specimen was worn possibly by fluvial transport or by digestion by a carnivorous animal before deposition. Thus, it is difficult to take precise measurements directly from the original specimens, but approximate measurements indicate size comparable to those specimens from UTEP and MNM. TMM has more *Aztlanologus* specimens than those studied by Winkler and Tomida (1988), including a few cut-and-polished teeth. We found 10 adult p3s in total, although in three of them it was not possible to identify either an enamel lake or open PIR. Fortunately, seven other specimens are better preserved and all possess enamel lakes (Tab. 1). One of them (TMM 40682-76A), which is the same tooth as TMM 40682-514 (Winkler and Tomida 1988: fig. 2A; Text-fig. 4e) is a cut-and-polished specimen, so its line drawing shows a nearly original enamel pattern. One specimen from batch TMM 40682-363 (13 teeth included in the same number) shows an enamel lake at the position of

AIR, as seen on specimens (MNM 5689-78-18 and MNM 5689-98-1) mentioned above.

Also, we found 10 p4–m2 adult specimens and confirmed that one (TMM 40682-76B, cut-and-polished specimen) possesses AER (Text-fig. 4f, Tab. 1). The depth of AER of this specimen is somewhat shallower than those of p4–m2 of the type specimen, but the shape and position are typical. On the other hand, the AER of TMM 40682-635 (Winkler and Tomida 1988: fig. 2B) differs from other specimens in shape and size. YT and AJW reexamined the specimen and concluded that the figure was inaccurate, and that this specimen does not possess the AER.

Aztlanologus from 111 Ranch (Blancan), Arizona is a single right p3 (Text-fig. 4g; also see Tomida 1987, Winkler and Tomida 1988). It possesses an enamel lake at the position of PIR. Although it is located at the lingual edge of the tooth, the enamel forms a ring, and is not open as a reentrant angle.

Although Winkler and Tomida (1988) mentioned the possibility that *Aztlanologus* from Fyllan Cave and 111 Ranch may be different species from the younger material described by Russell and Harris (1986), here we consider that all specimens from the three different horizons belong to a single species because the enamel patterns of p3s and p4–m1 are so similar to each other and the tooth size of the specimens is within the size range of those from the youngest deposits (Winkler and Tomida 1988: tab. 1). Based on the description above, it may be concluded that within this lineage, from ca. 2.5 Ma to ca. 30 ka, the PIR of p3s is always an enamel lake (100 %), while the presence of AER on known p4–m2 is about 10 to 14.5% for the last ~0.7 million years (Tab. 1).

m2 out of a complete type series (Čermák, pers. comm., Sept. 9, 2024).

One specimen (No. 651377; Daxner and Fejfar 1967: fig. 4a), a partial maxilla with dentition, shows the position of the palatal fossa, but the entire palatal bridge is not preserved. Thus, the length/width ratio of the palatal bridge is not available.

Other species of *Pliopentalagus* from China and Japan

In addition to the three species of the genus *Pliopentalagus* from Dajushan in Anhui Province, China (Text-fig. 2), two more species have been described from China: *Pliopentalagus nihewanensis* from the Late Pliocene of Hebei Province (Cai 1989) and *Pliopentalagus progressivus* from the Late Pliocene or Early Pleistocene of Henan Province (Liu and Zheng 1997). Tomida and Jin (2005) reexamined the material of *Pl. nihewanensis* in detail, and provided detailed illustrations of the teeth. The lower p3 (holotype) has greatly reduced crenulations on the posterior walls of PIR and PER, and AIR is very shallow (and disappears in basal view). It can be interpreted as a species of the genus *Trischizolagus* RADULESCO et SAMSON, 1967 having p3 with a most complicated enamel pattern. Two lower molariform teeth (p4–m2) lack any definitive characteristics. Thus, Tomida and Jin (2005) concluded that p3 should be reassigned as *Trischizolagus nihewanensis* (CAI, 1989), and p4–m2 should be considered Leporidae gen. et sp. indet.

Pl. progressivus is represented by a single p3 and a single p4 or m1, which is the largest among the known species of the genus. We consider it as a valid species of the genus, based on its general morphology of p3 and fairly well crenulated anterior thin enamel wall of the talonid of p4 or m1. However, detailed reexamination of p3 indicates that the morphology of part of PIR and AIR is unclear, and that cutting-and-polishing is necessary in order to obtain the clear enamel pattern of p3. In addition to the unclear part of PIR and AIR, a more rounded outline with much wider talonid in p3 (compared with a more rectangular outline with less wide talonid in p3s in other species) indicates that its evolutionary relationship with other species is unclear.

Tomida and Takahashi (2023) described the newest species, *Pl. okuyamai*, from the middle Pliocene (ca. 3.5 Ma) in central Japan. The holotype is a fragmentary skull with nearly complete upper dentition and palate, but no lower dentition. However, P3–M2 possess the secondary folds of the internal reentrant which are very deep and densely arranged (10 to 12 secondary folds on both anterior and posterior walls). P2 possesses three anterior reentrants with the main anterior reentrant deepest and well crenulated. These characters are sufficient to assign it to the genus *Pliopentalagus* without evidence from the lower dentition. Additional characteristics include, (1) it is the largest among the known species and is nearly equal in size to *Pentalagus furnessi* (STONE, 1900); (2) the general outline of P3–M2 is less rectangular (more square) than other species; and (3) the length/width ratio of the palatal bridge is the greatest among the known species of the genus and is almost the same as that of *Pentalagus furnessi*. Thus, Tomida and Takahashi (2023) concluded that *Pl. okuyamai* may be an ancestral form of *Pentalagus furnessi* (Text-fig. 5).

Systematic paleontology

Family Leporidae FISCHER, 1817
Subfamily Leporinae FISCHER, 1817

Genus *Pliopentalagus* GUREEV et KONKOVA
in GUREEV, 1964

Synonym. *Aztlanolagus* RUSSELL et HARRIS, 1986.

Type species. *Pliopentalagus moldaviensis* GUREEV et KONKOVA in GUREEV, 1964.

Original diagnosis. See Gureev (1964: 129).

Emended diagnosis. (Emended after Tomida and Jin 2009.) Body size small to medium; diastema of lower jaw short; lower incisor terminates more anteriorly than *Hypolagus*; enamel crenulations of reentrants on cheek teeth complicated; p3 possesses all five reentrants (counting enamel lake as a modification of PIR); posterior walls of PER and PIR (or enamel lake) thin and well crenulated; PIR on p3 always isolated as an enamel lake in primitive species, and ratio of the presence of enamel lake decreases in advanced species; p4–m2 with anterior wall of talonid well and deeply crenulated but not as deep as in *Pentalagus*, and with small AER in majority of the population in primitive species; length of palatal bridge relatively long in primitive species and becomes shorter in one lineage and longer in another lineage; P3–M2 with internal reentrant fold deep and enamel crenulations of both anterior and posterior walls deep and heavy but less than in *Pentalagus*.

Included species. *P. huainanensis* JIN, 2004, late Late Miocene, China (Anhui Province); *P. dajushanensis* TOMIDA et JIN, 2009, Early Pliocene, China (Anhui Province); *P. anhuiensis* TOMIDA et JIN, 2009, Late Pliocene, China (Anhui Province); *P. dietrichi* (FEJFAR, 1961; originally described as the genus *Alilepus*), late Early Pliocene (MN 15), Europe; *Pliopentalagus okuyamai* TOMIDA et TAKAHASHI, 2023, ca. 3.5 Ma (middle Pliocene), Japan; *P. progressivus* LIU et ZHENG, 1997, Early Pleistocene, China (Henan Province); and *P. agilis* (RUSSELL et HARRIS, 1986; originally described as the genus *Aztlanolagus*), Pleistocene – Holocene (?), North America (Arizona, New Mexico, Texas, Mexico).

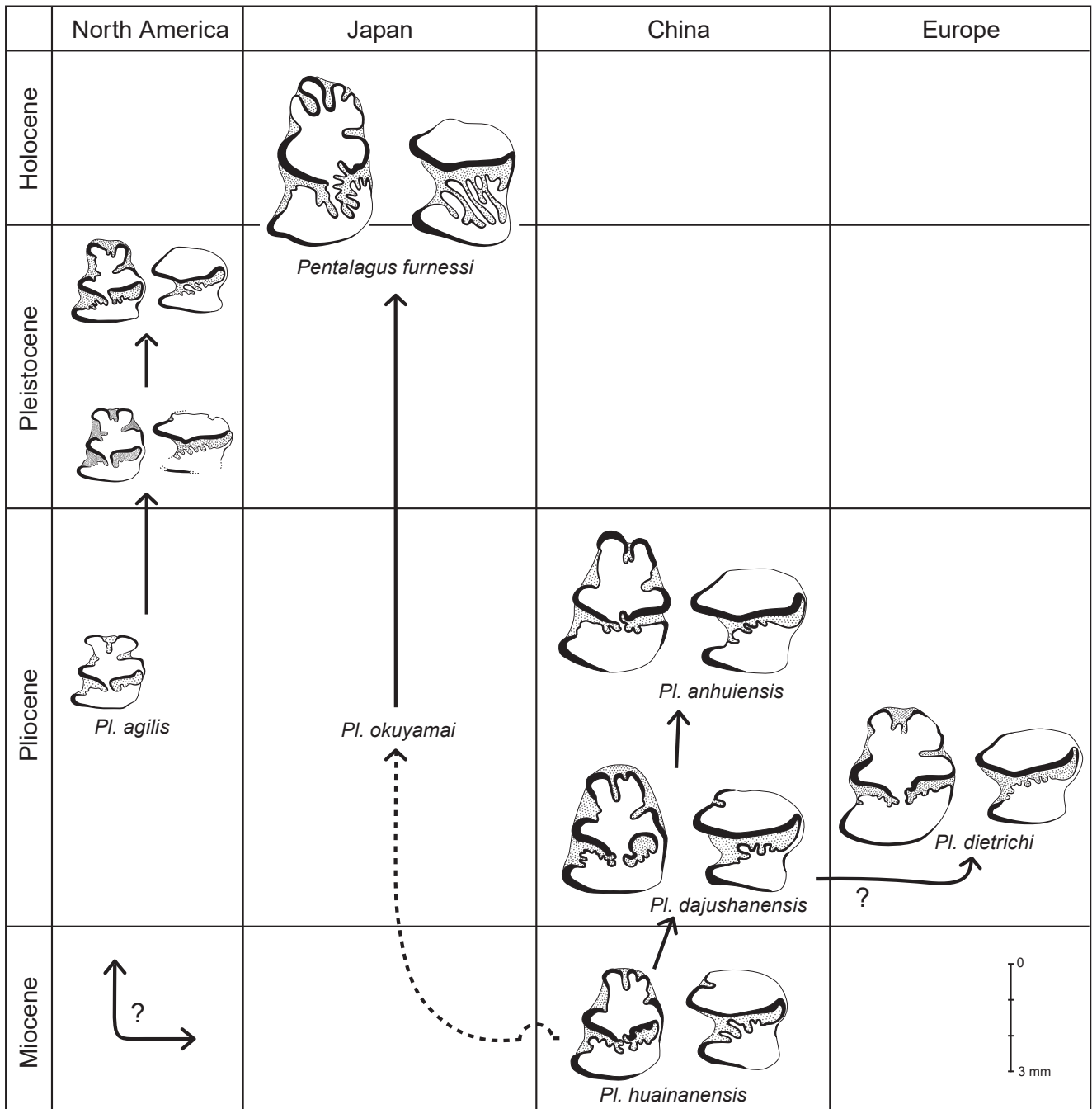
Occurrence. From the late Late Miocene to late Pliocene in Asia, Early Pliocene in Europe, and from the earliest to latest Pleistocene, Holocene? in North America.

Discussion: dynamic evolution of *Pliopentalagus*

Based on the discussion and review of all known species of the genera *Pliopentalagus* and *Aztlanolagus* above, we conclude that the genus *Aztlanolagus* should be synonymized with *Pliopentalagus*.

Place of origin and direction of dispersal of *Pliopentalagus*

As discussed so far, the oldest record of *Pliopentalagus* is *Pl. huainanensis* from Anhui Province, China in the latest Miocene (ca. 6 Ma). As far as known fossil records are concerned (Text-fig. 6), it appears that *Pliopentalagus*



Text-fig. 6. Proposed scenario of the evolution of *Pliopentalagus* based on the lower dentition. Symbol at the lower left corner indicates that the place of origin of the genus *Pliopentalagus* is unclear.

originated in China and dispersed to North America. However, crown group Leporidae were not present in the Old World until about 8 Ma: they differentiated in North America during the Early and Middle Miocene, and then dispersed to northern Asia in the Late Miocene around 8 Ma and afterward (the Leporid Datum of Flynn et al. 2013). Two alternative hypotheses may be possible: (1) *Pliopentalagus* originated in North America and dispersed to Asia before ca. 6 Ma (but after 8 Ma), and specimens of *Pliopentalagus* older than ca. 2.5 Ma have not yet been found in North America, or (2) *Pliopentalagus* originated in Asia from an unknown genus that dispersed from North America to Asia after 8 Ma, then dispersed again to North America most likely before *Pl. dajushanensis* evolved (because the frequency of the

enamel lake of p3 in *Pl. dajushanensis* is less than 100 %). The former hypothesis seems more likely, but there is no evidence to support it.

Evolutionary scenario

Based on the review and discussion of all known species above, we propose the following scenario for the dynamic evolution of *Pliopentalagus* (Text-fig. 6). If the genus originated in North America, it evolved over 6 Ma as a small species (*Pl. agilis*). If the genus originated in Asia, it evolved between 8 Ma and ca. 6 Ma, and then dispersed to North America and became a smaller species. The current record of *Pl. agilis* shows almost no change in size and morphology, including presence of an enamel lake at the position of PIR,

at least for the last ~2.5 million years. Change in frequency of AER on p4–m2 is unclear, but if it was as high as *Pl. huainanensis* at the beginning, it may have dropped to about 10–15% by the late Pleistocene.

If *Pl. huainanensis* evolved from a North American species (perhaps *Pl. agilis*), it evolved larger size. Three species known from the Dajushan in Anhui Province, China, form a single lineage (Dajushan lineage), and they evolved as follows: (1) size became larger gradually, (2) frequency of an enamel lake on p3 decreased from 100% to 84% and 33%, (3) frequency of AER on p4–m2 decreased from 71% to 66% and 29%, and (4) the length/width ratio of the palatal bridge decreased from 0.85 to 0.74 and 0.63. As mentioned above, the Dajushan lineage represents an example of phyletic gradualism.

Pl. okuyamai (or an unknown species ancestral to it) from Japan most likely evolved from *Pl. huainanensis* as early as ca. 6 Ma, because the length/width ratio of the palatal bridge is largest in *Pl. huainanensis* among the Dajushan lineage. Although there is no fossil record up to ca. 3.5 Ma in Japan, the evolution of *Pl. okuyamai* included (1) an increase in size, (2) general outline of P3–M2 becoming less rectangular than in the Dajushan lineage, and (3) length/width ratio of the palatal bridge becoming as large as in *Pentalagus furnessi* (Text-fig. 5). Thus, *Pl. okuyamai* may be the closest ancestor of *Pentalagus*. However, although no lower teeth of *Pl. okuyamai* are known, *P. furnessi* possesses an enamel lake on p3 at 18% and no AER on p3–m2. These values suggest *P. furnessi* retains a tendency of those characters seen in the Dajushan lineage (Tab. 1).

Pl. dietrichi probably evolved from *Pl. dajushanensis* because of the similar geologic age (Early Pliocene). However, the former lacks an enamel lake on p3 and an AER on p4–m2, while the latter possesses an enamel lake on p3 at 84% and AER on p4–m2 at 66%. These differences may be explained as follows: the ancestor of *Pl. dietrichi* may have dispersed to Europe with a small population, and that population lacked an enamel lake on p3 and AER on p4–m2. Other than those two characters, *Pl. dietrichi* is quite similar to *Pl. dajushanensis* in morphology and average size of the teeth.

Conclusion

The genus *Azlanolagus* is synonymized with *Pliopentalagus* because the morphology of p3 and p4–m2 is quite similar (except for the size) and the length/width ratio of the palatal bridge is also similar, especially between *A. agilis* and *Pl. huainanensis* (most primitive known species of the genus). *Pliopentalagus agilis* basically did not change its general morphology and size, at least for the last about 2.5 million years. The place of origin of *Pliopentalagus* is unknown, but if it is of North American origin, it dispersed to China sometime between 8 Ma and ca. 6 Ma. Three species of *Pliopentalagus* evolved in the Dajushan in Anhui Province, China, and they form an evolutionary lineage which represents an example of sympatric phyletic gradualism. *Pl. okuyamai* (or an unknown species ancestral to it) from Japan most likely evolved from *Pl. huainanensis* as early as ca. 6 Ma, and it is a possible ancestral form of *Pentalagus furnessi*. *Pl. dietrichi* probably evolved from

Pl. dajushanensis simply based on their similar geologic age; the ancestor of *Pl. dietrichi* may have dispersed to Europe with a small population, which probably lacked a gene controlling the appearance of an enamel lake on p3 and AER on p4–m2. Thus, *Pliopentalagus* diversified and dispersed widely in the Holarctic region over the last 6 million years, and became extinct near the end of the Pleistocene, leaving a single descendant, *Pentalagus furnessi* in Japan.

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